BOTANICAL MUSEUM LEAFLETS

HARVARD UNIVERSITY

PRINTED AND PUBLISHED AT THE
BOTANICAL MUSEUM
CAMBRIDGE, MASSACHUSETTS

BOTANICAL MUSEUM LEAFLETS

HARVARD UNIVERSITY

VOLUME XIII

BOTANICAL MUSEUM
CAMBRIDGE, MASSACHUSETTS
1947–1949

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ERRATA

page 9, line 15
for *carriguda* read *barriguda*

page 28, line 22
for 994 read t. 994

page 47, line 21
for (*centaros*) read (*cantaros*)

page 58, line 30
for *eti hua* read *e ti hua*

page 164, lines 4 and 19
for Cuezcomayxtlahuacan read Cuezcomaixtlahuacan

page [201], Plate XVII
for A read B; for B read C; for C read A

Issued June 27, 1949

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, SEPTEMBER 8, 1947 VOL. 13, NO. 1

STUDIES IN THE GENUS HEVEA I

BY

RICHARD EVANS SCHULTES [1]

1. THE DIFFERENTIATION OF HEVEA MICROPHYLLA AND H. MINOR

IN 1899, Hemsley described and illustrated an unusual species of *Hevea*, naming it *H. minor* because of its small stature. The species was based upon fruiting material collected by Richard Spruce on the Río Casiquiare in southern Venezuela.

A few years later, in 1905, Ule described *Hevea microphylla*, basing the species upon fruiting material which he had collected on the lower Rio Negro in Brazil. Five years later, the monographer Pax published variety *typica* and variety *major* of this concept.

In 1906, Huber (Bol. Mus. Goeldi 4 (1906) 633–634) suggested that *Hevea microphylla* might be synonymous with *H. minor*, pointing out several characters in which the two concepts, as described, agree. He admitted, however, that there seemed to be differences in other characters, so he chose "to consider *H. microphylla* a distinct species for the present." Identifying a flowering collection made by Ducke (*Ducke 7027*) in the lower Rio

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Negro as representing *Hevea minor*, Huber published an amplified description of this species, which included a description of the flowers of the Ducke specimens (loc. cit. 634-635). He indicated that the two species appeared to be closely allied, although the flowers of *Hevea microphylla* were not known. In 1913, Huber still maintained them as distinct concepts, including them with *Hevea brasiliensis* (HBK.) Muell.-Arg. in his series *Intermediae* as he had done previously (loc. cit. 622), but intimating that further studies might make it necessary to remove *H. microphylla* and *H. minor* from series *Intermediae* (he considered series *Luteae* and *Intermediae* to represent provisional classifications and not natural groups) and, together with *H. rigidifolia* (Spruce ex Bentham) Muell.-Arg., to form a new group (Bol. Mus. Goeldi 7 (1913) 202).

Apparently accepting Huber's determination of his flowering collection (*Ducke 7027*) as *Hevea minor*, Ducke, who had collected topotype material of *H. microphylla* (*Ducke HJBR 23750*) which agreed in all characters with *Ducke 7027*, reduced *H. microphylla* and *H. microphylla* var. *major* to synonymy under *H. minor* (Arch. Instit. Biol. Veget. 2, no. 2 (1935) 242). Recently, he has maintained this opinion (Bol. Teen. Instit. Agron. Norte no. 10 (1946) 20). Baldwin enumerated nine species which he accepts as valid: he includes *Hevea minor* but makes no mention of *H. microphylla*, thereby suggesting agreement with Ducke's treatment of the latter as representing the same concept as the former (Journ. Hered. 38, no. 2 (1947) 54.

While engaged in a study of *Hevea* in the Kew Herbarium in June, 1947, I was able to consult the type of *H. minor* (*Spruce 3457*) as well as a sterile duplicate type (*Ule 6025*) and a topotype (*Ule 6023*) of *H. microphylla*. It is now apparent that *Hevea minor* and *H. microphylla*

represent two distinct entities. It is also evident from a comparison of *Ducke 7027* and *Ducke HJBR 23750* with the type material that the two Ducke collections represent *H. microphylla*. This being so, the flowers which Huber described in his amplified description of *Hevea minor* (Bol. Mus. Goeldi 4 (1906) 634–635) are actually flowers of *H. microphylla*. *Hevea minor* is still known only from the type collection which is in fruit.

It is unfortunate that the misinterpretation of these two concepts has become so firmly established in *Hevea* literature. The following observations are presented with the hope that they may lead towards clarification.

The seed and capsule of the type of *Hevea minor* were very accurately illustrated by Hemsley in conjunction with his original description of the species (Hooker's Icon. Pl. (1899) t. 2572). Perfectly complanate-ovoid with two very conspicuous flat surfaces ventrally and a very pronounced ridge dorsally, the seed measures 15 mm. long, 9 mm. thick, 11–12 mm. wide. The valves of the capsule, which have an unusually thick ligneous endocarp—nearly 3 mm. thick—in relation to their overall size are only slightly contorted due to dehiscence; they measure 26 mm. long, 11 mm. deep. The epicarp of the capsule is apparently extremely thin in life. The capsule itself is perfectly globose with very little trace of a trisulcate condition, is not apically pointed, and measures about 25 mm. long and 25 mm. in diameter. It is borne on a slender peduncle about 4 cm. in length.

Similarly, an adequate description and a clear illustration of the critical structures of *Hevea microphylla* are available (Engler Bot. Jahrb. 35 (1905) 668, t. 1: k, l). The seed is rather large, measuring, according to the type description, 20–25 mm. long, 12–15 mm. thick, and would suggest, in many respects, the smaller seeds of *Hevea Spruceana* (Benth.) Muell.-Arg. It is peculiarly

obovoid, much wider at the base than at the apex, is subquadrangular in cross section, has obsolete flat surfaces ventrally and absolutely no ridge dorsally. The seeds which accompany the topotypical specimen *Ducke* ***H.J.B.R.*** *23750*, which is, indeed, a very close match for *Ule 6023* and *6025*, are in complete agreement with those described by Ule and measure 25–28 mm. long, 15–16 mm. thick, 17–18 mm. wide at the widest point. The valves of *Ducke H.J.B.R. 23750* are large, measuring up to 45 mm. in length. They have an extraordinarily thin endocarp which is only 0.3 mm. thick! In dehiscence, they twist very tightly, due probably to the almost papery consistence of the endocarp. If we are to judge from Ule's figure, the capsule of *Hevea microphylla* is elongate-ovoid-pyramidal with a very acute apex, slightly trisulcate with a conspicuous dorsal keel in each carpel, 40–50 mm. long, 30–40 mm. in diameter. It is borne on a robust peduncle 6–7 cm. long.

There appear to be no significant distinguishing characters in the leaves of the two concepts except that the leaves of *Hevea minor* are definitely concolorous, whereas those of all collections of *H. microphylla* are very discolorous. Floral characters which might further separate them will not be available until *Hevea minor* is found in flower. I believe that the seeds of the two are so utterly distinct in size and shape that we are justified in regarding them as distinct species.

There are no valid reasons whatsoever for Pax's creation of *Hevea microphylla* var. *major*. Pax gives as his basis for the variety "foliola majora, angustiora," but *Ule 6023* and *6025* as well as *Ducke 7027* and *Ducke H.J.B.R. 23750* show all possible intergradations in the size of the leaflets, and this is known to be a character of little taxonomic value in *Hevea*. It is clear that the description of *Hevea microphylla* var. *major* is the de-

scription of an individual collection and does not represent a biological entity.

Were the confusion which has been created by the reduction of *Hevea microphylla* to synonymy under *H. minor* confined to nomenclature, it would probably not be so urgently in need of clarification. It has led to serious misunderstanding of the fundamental biology of the two plants.

When Hemsley described *Hevea minor*, his basic diagnosis was: "pro genere omnibus partibus parvis, seminibus albis immaculatis," and, following the description, he observed: "This is so very distinct in the smallness of all its parts, and particularly in its small white seeds, that we have not hesitated to establish it on incomplete material." Later, Pax emphasized this unusual condition of the seed when he wrote, under *Hevea minor:* ". . . . semina laevia, immaculata, triangulari-oblonga, alba. . . ." (Engler Pflanzenr. 4, 147 (1910) 125). Hemsley and Pax, both without field experience in *Hevea* studies, had not realized that the seeds which they were describing were white and without spots because they were unripe. Huber had pointed this out in 1906 (Bol. Mus. Goeldi 4 (1906) 633), explaining that he had noted in his own field work with *Hevea brasiliensis* and other species that unripe fruits can ripen and even open after separation from the tree, in which case the seeds do not develop normally. The fact that the seeds of the type specimen of *Hevea minor* were unripe was also stated by Ducke (Arch. Instit. Biol. Veget. 2, no. 2 (1935) 242). I have examined the seeds carefully and, basing my judgment on field experience in the collection and study of several tons of seed of *Hevea brasiliensis*, find that, while they were slightly short of complete maturation when Spruce collected the specimen, the hardness of their testa and their fully rounded out appearance are convincing evi-

dence that full size, or very nearly so, and mature shape had been obtained. These, after all, are the characters of fundamental significance; the type of coloration which the seed would have had when ripe is of much lesser importance.

It is necessary to consider the mode of dehiscence of *Hevea minor* and *H. microphylla* because great significance has been placed on this in the classification of the genus.

Ducke (Arch. Instit. Biol. Veget. 2, no. 2 (1935) 243) interpreted the fruit of *Hevea minor* as follows: "This species was created . . . . on a specimen . . . . without flowers and with no mature capsule (the seeds are still white!) but sufficiently characterized by the form of the leaves and chiefly by the form, the consistence and the slow dehiscence of the capsule (see the half-opened capsule reproduced in Hemsley's work, a feature which would be impossible in the case of any other known *Hevea* species)." In his key to the species of *Hevea*, Ducke (loc. cit. 225) says of *H. minor:* "Capsule . . . . opens with a slow dehiscence and lets the seeds fall in the water; the capsule then twists itself and remains for a long time adherent to the pedunele . . . ." He separates *Hevea minor* from all other species on the basis of the presumed slow dehiscence of the capsule of the former as against an explosive shedding of seed in the latter (loc. cit. 221). This erroneous stand results from the belief that *Hevea minor* and *H. microphylla* are one and the same.

Judging from the structure of the thick, woody valves of the capsule of *Hevea minor*, the capsule opens, as in all other species with comparably strong valves, more or less explosively. The valves are not strongly twisted, due to their shortness and their extremely strong ligneous endocarp which measures, as stated above, up to 3 mm.

in thickness. They may dehisce as in some specimens of *Hevea Spruceana* where the explosion is less violent than in most other species, but the structure of the valves indicates definitely that dehiscence is explosive. The "half-opened fruit" drawn by Hemsley's artist and actually preserved in that state on the herbarium sheet is due, I believe, to the fact that, as shown by the whiteness of the seeds, the capsule was not quite mature and that the artificial heat applied in making the dried specimen caused it to open partially while still under pressure in the plant press. This has often occurred when I have been drying *Hevea* specimens by means of artificial heat. Unless we can find some definite evidence of slow opening and gentle dropping of the seed in *Hevea minor*, we are making an unsound assumption in believing that such a mode of dehiscence is normal.

In *Hevea microphylla*, however, there is indeed very strong evidence that slow dehiscence is the rule, for the entire structure of the valves is distinct and is such that a violent opening and shedding of the seeds would be mechanically impossible. The valves are provided with an excessively thin—0.3 mm.—endocarp which is coriaceous, not even woody. Clearly, this structure is too weak to build up the tension necessary for a violent bursting. The valves open slowly, as Ducke has pointed out, and let the seeds drop slowly to the ground, persisting for some time on the peduncle (as often is the case in *Hevea Spruceana*) and then, when the seed is shed, twist themselves rather tightly due to their almost papery consistence. This is indeed unusual in the genus.

There would appear to be a strong ecological differentiation between *Hevea minor* and *H. microphylla*. The former is known only from the dry, sandy scrub-forest or caatinga of the Casiquiare. The latter, so far as available collections indicate, inhabits forests which are peri-

odically subject to very deep flooding. Spruce does not give us in his notes any indication of the shape of the trunk of *Hevea minor*, stating merely: "Arbor parva, 15 pedalis." If the trunk had deviated from a normal cylindrical shape, this careful observer would certainly have noted the fact. *Hevea microphylla* responds to its flood habitat by producing a swollen or bellied trunk, and it is called *seringa barriguda* (=bellied rubber) by the natives of São Joaquim on the Rio Negro, the same common name which is applied to *H. Spruceana* (Ducke: Bol. Tecn. Instit. Agron. Norte no. 10 (1946) 21).

Clavis specierum Heveae minoris et H. microphyllae:

A. Arbor parva 15 pedalis, cum trunco probabiliter cylindrico, in caatinga occurrens. Folia concoloria. Capsula perfecte globosa, 25 mm.×25 mm., cum pedunculo subgracili, 40 mm. longo; valvis 26 mm. longis, vix contortis, endocarpio lignoso, usque ad 3 mm. crasso. Semina parva, complanato-ovoidea, 15 mm.× 9 mm.×11–12 mm., carina dorsali conspicua. Dehiscentia probabiliter explodens.

1. *Hevea minor*

AA. Arbor parva vel mediocris, cum trunco infra incrassato, in sylvis profunde inundatis occurrens. Folia discoloria. Capsula ovoideo-pyramidalis, apice valde acuta, 40–50 mm.×30–40 mm., cum pedunculo robusto, 60–70 mm. longo; valvis 45 mm. longis, valde contortis, endocarpio vix coriaceo, valde tenuissimo, 0.3 in diametro. Semina magna, elongato-obovoidea, subquadrangularia, 20–28 mm.×12- 16 mm.×17–18 mm., ecarinata. Dehiscentia ut videtur lenta.

2. *Hevea microphylla*

1. Hevea minor *Hemsley* in Hooker's Icon. Pl. 26 (1899) tab. 2572; Pax in Engler's Pflanzenr. 4, 147 (1910) 125.

Venezuela: Río Casiquiare, "in sylvis humilioribus. Arbor parva, 15 pedalis. Siphonia." *Richard Spruce 3457* (Typus Herb. Kew). [In Spruce's field note-book, preserved at Kew, the following annotations appear: "3457. Siphonia – Casiq. Caatinga. Sm. tree 15 ft. Lts. sm. lanc. acum. obt. Frt."]

2. Hevea microphylla *Ule* in Engler's Bot. Jahrb. 35 (1905) 669, tab. 1: j, k, l, m; Ule in Kautschukgewinnung (Kolonialwirtsch. Kom. 1905) (1905) 10; Huber in Bol. Mus. Goeldi 4 (1906) 634 pro parte [non accurate, sub *Hevea minore*], 636; Pax in Engler's Pflanzenr. 4, 147 (1910) 125; Ducke in Arch. Instit. Biol. Veget. 2, no. 2 (1935) 241 pro parte, tab. pag. 246, a–f, 247, a–b [non accurate, sub *Hevea minore*]; Ducke in Bol. Técn. Instit. Agron. Norte, no. 10 (1946) 20 pro parte.

Hevea microphylla *Ule* var. typica *Pax* in Engler's Pflanzenr. 4, 147 (1910) 126.

Hevea microphylla *Ule* var. major *Pax* in Engler's Pflanzenr. 4, 127 (1910) 126.

Brazil: Estado do Amazonas—Rio Negro. "Inseln Xiparú, São Joaquim. [Nom. vulg. =] *seringa serapó*. *E. Ule 6023*, February 1902 (Herb. Kew).—"Inseln Xiparú, São Joaquim. [Nom. vulg. =] *carriguda*. *E. Ule 6024*, February 1902 (Typus *Heveae microphyllae* var. *majoris* non vidi).—"Inseln Xiparú, São Joaquim. [Nom vulg. =] *tambaqui seringa*." *E. Ule 6025*. February 1902. (Typus duplicatus Herb. Kew).—"Barcellos." *A. Ducke 7027*.—"Insula Xiparú, prope São Joaquim . . . . silva profunde inundata. Arbores (3 ex.) parvae vel mediocres, trunco infra incrassato, flor pallide luteis. [Nom vulg. =] *seringa tambaqui* vel *seringa barriguda*." *A. Ducke Herb. Jard. Bot. Rio 23750*, August 8, 1931 (Topotypus Herb. Kew; U.S. Nat. Herb.).

2. A NEW INTERPRETATION OF HEVEA NITIDA AND ITS VARIETY

Hevea nitida *Martius ex Mueller-Argoviensis* in Martius Fl. Bras. 11, pt. 2 (1874) 301.

Siphonia nitida Martius ex Mueller-Argoviensis loc. cit.

Hevea viridis Huber in Bull. Soc. Bot. France 49 (1902) 48; emend. in Bol. Mus. Goeldi 7 (1910) 235.

In his forthcoming "A Study of Hevea with its economic aspects in the Republic of Peru," Dr. Russell J. Seibert reduces *Hevea viridis* to synonymy under *H. nitida* on the basis of new characters which he has found

to be of great value in the classification of the species of this genus.

Hitherto, (in Bot. Mus. Leafl. Harvard Univ. 12 (1945) 7) I have believed *Hevea nitida* to represent the concept which Ducke described as *H. brasiliensis* (HBK.) Muell.-Arg. var. *subconcolor*. I am now, however, in complete agreement with Seibert's point of view that *Hevea nitida* is a distinct concept representing the same species as that which has been known as *H. viridis*.

Seibert writes: "They [certain specimens of *Hevea viridis*] appear to represent topotypical cultivated material from Huber's type locality of *H. viridis*. The one flowering collection made by Archer is quite referable to *H. nitida* in floral morphology, the short-shoots, and in general, the leaflets. The lower leaf surfaces of this and other specimens of the cultivated plant, however, tend to show a minute lepidote condition slightly atypical of *H. nitida*. The scales, notwithstanding, are neither of sufficient size nor density to affect the concolorous aspect. There remains some question, since the leaflets do show a slight *H. brasiliensis* aspect, whether or not Huber's *H. viridis* had some admixture of *H. brasiliensis* germ-plasm.

"Through the excellent photograph (made by the Chicago Field Museum) of the entire type specimen of Martius' collection deposited in the Herbarium at Munich, it has been possible to identify *H. nitida* with *H. viridis* with some degree of certainty. The presence of interflush short-shoots as well as the glossy under surface of the leaflets leaves little doubt that *H. viridis* should henceforth be referred to *H. nitida*."

In view of this new understanding of *Hevea nitida*, it is necessary to alter the name of the diminutive, shrubby *Hevea*, described as *H. viridis* var. *toxicodendroides*

from the ancient remnant quarzite hills of the Apaporis-Vaupés area of Colombia.

Hevea nitida *Martius ex Mueller-Argoviensis* var. **toxicodendroides** (*R. E. Schultes et Vinton*) ***R. E. Schultes comb. nov.***

Hevea viridis Huber var. *toxicodendroides* R. E. Schultes et Vinton in Caldasia 3 (1944) 25.

"*Hevea toxicodendroides* R. E. Schultes ex P. H. Allen in Mo. Bot. Gard. Bull. 32 (February, 1944) 50; *nomen nudum.*

AN ERRONEOUS RECORD OF HEVEA IN COLOMBIA

BY

A. H. G. Alston[1] and Richard Evans Schultes[2]

In Rees' "Cyclopedia" (39 (1819) sub *Siphonia*), there is a most interesting reference to a Mutis collection of *Hevea guianensis* Aubl. ("*Siphonia elastica*") from Colombia. Sir J. E. Smith, who compiled the section of the encyclopedia on *Siphonia*,[3] wrote: "There is, indeed, in the Linnaean herbarium, besides the original specimen,[4] marked with this last name [*Siphonia elastica*], another from Mutis, which that learned botanist judged to be a distinct species, though affording, as some other trees do, a similar gum. The leaflets in this specimen are larger, more acute at each end, and destitute of partial stalks. The calyx is nearly half an inch long. The

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[3] Lady Smith: "Memoir and correspondence of the late Sir James Edward Smith, M.D." 1 (1832) 488–489; B. D. Jackson: "An attempt to ascertain the actual dates of publication of the various parts of Rees' Cyclopedia" (1895) 3.

[4] This statement undoubtedly refers to a specimen of *Hevea guianensis* preserved in the Linnaean Society in Smith's herbarium. From all appearances of the specimen, it is one of the Aublet collection from French Guiana and represents the type of the genus.

younger Linnaeus, in his *Supplementum* 422, promised to publish something at a future time respecting the various trees that yield an elastic gum of the same utility as the *Caoutchouc;* but he did not live to execute his design."

From the point of view of the taxonomic history of *Hevea*, the genus of the Pará rubber tree, the existence of a Mutis specimen would be of the utmost significance. It would represent the earliest known collection of the genus from Colombia, the northwesternmost sector of its range. A Mutis specimen would also be of extreme importance as it would alter our understanding of the distribution of *Hevea*, for, so far as we are aware, no Mutis material was collected in those parts of the Amazon and Orinoco drainage areas where the genus is known to occur.

For these reasons, we consulted the Mutis material to which Smith made reference and which is preserved in Linnaeus' herbarium at the Linnaean Society. The specimen, included in the *Jatropha* folder, is not a *Hevea* but represents the rutaceous *Cusparia trifoliata* (Willd.) Engler,[5] the type of which was collected in Venezuela.

Comprising several leaves and an inflorescence of fertilized flowers from which the corollas have dropped, the specimen is mounted upon paper bearing a Spanish watermark. In the upper right corner of the sheet, there is, in Mutis' handwriting, a figure "89." At the bottom of the sheet, the elder Linnaeus had written "Hevea" on one line and "elastica" below it, an epithet which has never been published. The younger Linnaeus scratched out the word "Hevea" and substituted "Jatropha," but he did not cite the collection in his *Supplementum 422* under *Jatropha elastica* to which concept he reduced

[5] Tabula in Humboldt. Plant. Aequin. 2 (1813) t. 97.

Aublet's *Hevea guianensis*. Elsewhere on the sheet, apparently in the elder Linnaeus' hand, there is an annotation "Gummi elastique."

A detailed search through the collection of Mutis' correspondence with Linnaeus, preserved at the Linnaean Society, revealed an enumeration of two shipments of plants from Colombia to Sweden. The specimen in question was included in the second shipment. We find that Mutis had made, under "89" in the enumeration of the specimens of this shipment, the following interesting annotation: "Pro Chinchona habita ab incolis guyanae." Even though the term *guyana* was rather loosely employed in this early period to designate much of southern Venezuela and the Orinoco basin, it has been impossible for us to ascertain Mutis' source for this statement. It is, of course, highly significant as an observation, because *Cusparia trifoliata* is the source of Angostura-bitters and has been used rather widely in South American folk-medicine as a febrifuge. Humboldt states that "On the coasts of New Andalusia, the cuspa is considered as a kind of Cinchona." [6]

Further study of Mutis' correspondence has failed to shed any light on Linnaeus' source for his annotation "Gummi elastique." It is most probable, in our opinion, that the note was added somewhat casually for the benefit of students after the plant had been determined, to Linnaeus' apparent satisfaction, as representing the concept now known as *Hevea guianensis*. *Cusparia trifoliata*, of course, is not a latex-bearing plant.

There is an additional annotation on the sheet. It is in pencil, apparently in the handwriting of Smith, and states that the specimen is markedly different from a sterile specimen from Brazil which Linnaeus had likewise

[6] Personal Narrative (translated by H. M. Williams) 3 (1822) 27.

annotated "Gummi elastique" but which had not been labelled with a Latin epithet. This Brazilian specimen[7] is neither *Jatropha* nor *Hevea* but, curiously, would seem also to be a rutaceous plant, *Esenbeckia febrifuga* (St. Hil.) Mart., likewise a source of bitters and often, in an earlier period, used to adulterate or falsify true Angostura-bitters. It naturally does not represent a lacticiferous plant, and the annotation with reference to gum elastic is as erroneous as the analogous annotation on the sheet of the Mutis specimen of *Cusparia trifoliata* and was undoubtedly made for the same purpose.

We wish to express our appreciation to Spencer Savage, Esq., Assistant Secretary of the Linnaean Society, for his very kind help in the study which has led to the clarification of the erroneous record of a Mutis collection of *Hevea*.

[7] The Brazilian specimens in the herbarium of Linnaeus were probably collected by Joaquim Velloso de Miranda (1733–1815) and sent to Linnaeus by Domenico Vandelli (1735–1816). He collected in Minas Geraes.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, NOVEMBER 19, 1947 VOL. 13, NO. 2

COMMENTARIES ON SPIRANTHES. I

BY

OAKES AMES

I. SPIRANTHES TUBEROSA SENSU FERNALD

IN JANUARY 1946[1], Professor M. L. Fernald resurrected from outdated literature the obscure species *Spiranthes tuberosa* Raf. (1833), type specimens of which are not known to exist. In seeking some element in our flora with which this ambiguous Rafinesquian product, interpreted by a twenty-one word description, might be specifically identical, Fernald hit on the "white lipped *S. Beckii* Lindl." (1840), stating that there was certainly no doubt about it. He failed, however, to explain how he discovered that *S. tuberosa* had a white lip. Rafinesque certainly gave no clue, for, in his brief description, he dismissed the lip with just two descriptive terms. He used the words "*cuneato acuto*," which do not apply to the lip of any known species of Spiranthes in the flora of the United States. Fernald claimed that *S. tuberosa* not only is identical with and antedates *S. Beckii* Lindl., but is also the characteristic species described in 1867 by Asa Gray as *S. simplex* (a homonym of *S. simplex* Grisebach and a synonym of *S. Grayi* Ames).

In August 1946[2], Fernald discussed the identity of *Spiranthes tuberosa* at greater length. He showed that,

[1] Rhodora 48 (1946) 10.

[2] Rhodora 48 (1946) 189.

from the bibliographic evidence, *Spiranthes Beckii* Lindl. "taxonomically" was as hopeless a muddle as could be imagined since it was concocted from elements of several different species. He pointed out in detail how Lindley, at a time when nomenclatural procedure was governed by less rigid rules than are now observed, adopted the specific name "Beckii" in violation of all obligations to the synonymy cited. Fernald, consequently, quite properly dismissed the name, *S. Beckii*, as being doubly illegitimate. He also recognized two strongly marked geographic variations in *S. tuberosa*, a southern one and a northern one. He assigned the species name to the southern element and reduced *S. Grayi* to varietal status for the northern element.

Actually and taxonomically *Spiranthes Beckii* is the ancient, well-established and well-known *S. gracilis* (Bigel.) Beck, which nomenclaturally antedates *S. tuberosa* by nine years. When John Lindley, in his "Genera and Species of Orchidaceous Plants" (1840), described *S. Beckii*, he cited two collections of specimens as being referable to it: one from Massachusetts (without collector), the other from Louisiana (Drummond 332). The type sheet of *S. Beckii* in Lindley's herbarium at Kew contains these two collections, and also a third consisting of two plants from Albany, New York, collected by Beck. As Lindley did not refer directly to these New York plants in his description, it may well be that they were acquired after 1840 and consequently should be excluded from any discussion of the Lindleyan type of *S. Beckii*. (It may be noted, however, that camera-lucida drawings of the lips of the New York plants, made by Victor S. Summerhayes, show that in outline and neuration they exemplify *S. gracilis* (Bigel.) Beck).

The Massachusetts specimen on the type sheet (collector unknown) is accompanied by the following note:

Spiranthes aestivalis var. gracilis Torr. mss.
S. gracilis Beck
Neottia gracilis Bigelow fl. bost. ed. 2.
This hardly differs specifically from S. aestivalis. The common variety not infrequently bears a small ovate radical leaf. Massachusetts.

Mr. Summerhayes has also made for me a camera-lucida drawing of the lip of this Massachusetts plant. There can be no doubt about its being typical *S. gracilis*. Indeed, when Asa Gray described *S. simplex* in 1867, in the fifth edition of "The Manual," he was familiar with Lindley's type of *S. Beckii* and referred the latter species to *S. gracilis*, "at least as to the northern plant." This reference to the northern plant was made because the type sheet of *S. Beckii* also carried the specimens from Louisiana.

In our discussions of the components of Lindley's illegitimate *S. Beckii* we must give close attention to these Louisiana collections made by Drummond in 1832 near New Orleans, especially so since Asa Gray believed Drummond's 332 to represent plants that were different from the northern *S. gracilis*. In the Gray Herbarium there is a duplicate of Drummond's collection annotated by Gray as *S. Beckii*. In 1904, I accepted this Drummond plant as being referable not only to *S. Beckii* Lindl., but as being conspecific with *S. Grayi* Ames (*S. simplex* Gray, not Grisebach). More recent studies have proved that *S. Grayi* is a distinct species. I am indebted to V. S. Summerhayes again for his great kindness in sending me a carefully executed camera-lucida drawing of the lip of Drummond's 332 in the Lindley Herbarium. The Kew plant is identical with the duplicate in the Gray Herbarium and is clearly the same as the rather common southern Spiranthes recently recognized as *S. gracilis* var. *floridana* (Wherry) Correll.

Fernald has annotated the Drummond plants and sev-

eral other similar southern specimens in the Gray Herbarium, clearly referable to *S. gracilis* var. *floridana*, as typical *S. tuberosa* Raf. and these may be taken to indicate the strongly marked geographic variant to which he referred in "Rhodora"[3]. From a study of these specimens and of Professor Fernald's remarks, it is apparent that he has misidentified some of the southern representatives of *S. gracilis* and has treated them as conspecific with the slender forms of *S. Grayi* which range southward to Georgia, Alabama and Mississippi. Actually *S. gracilis* var. *floridana* is quite distinct from *S. Grayi*. It differs in the relatively narrower blade of the lip which is usually constricted near the apex and is conspicuously 5-nerved on the claw. The lip ranges between 3 mm. and 5 mm. in length. (The lip of the Drummond specimen, for example, is 3.4–4 mm. long.) The lip of *S. Grayi* in relation to its length is broader than the lip of *S. gracilis* var. *floridana*. In outline it is commonly broadly ovate, obtuse or rounded-quadrate, the average length being about 3 mm. The blade of the lip is white and rarely more than 3-nerved beyond the middle. It gives the impression of being 3-nerved on the claw and paucinervate above. The lip of *S. gracilis* var. *floridana* is yellow on the central portion. In the extreme South *S. Grayi* is a very rare species and some of the herbarium records that have been relied upon for reporting Florida stations should be restudied to ascertain whether or not they are actually based on variants of *S. Grayi* or on variants of *S. gracilis* var. *floridana*. Furthermore, the likelihood of hybridity should not be overlooked where *S. Grayi* and *S. gracilis* mingle.

In his reduction of *S. Grayi* to varietal rank, Fernald, as stated above, was influenced by the belief that *S.*

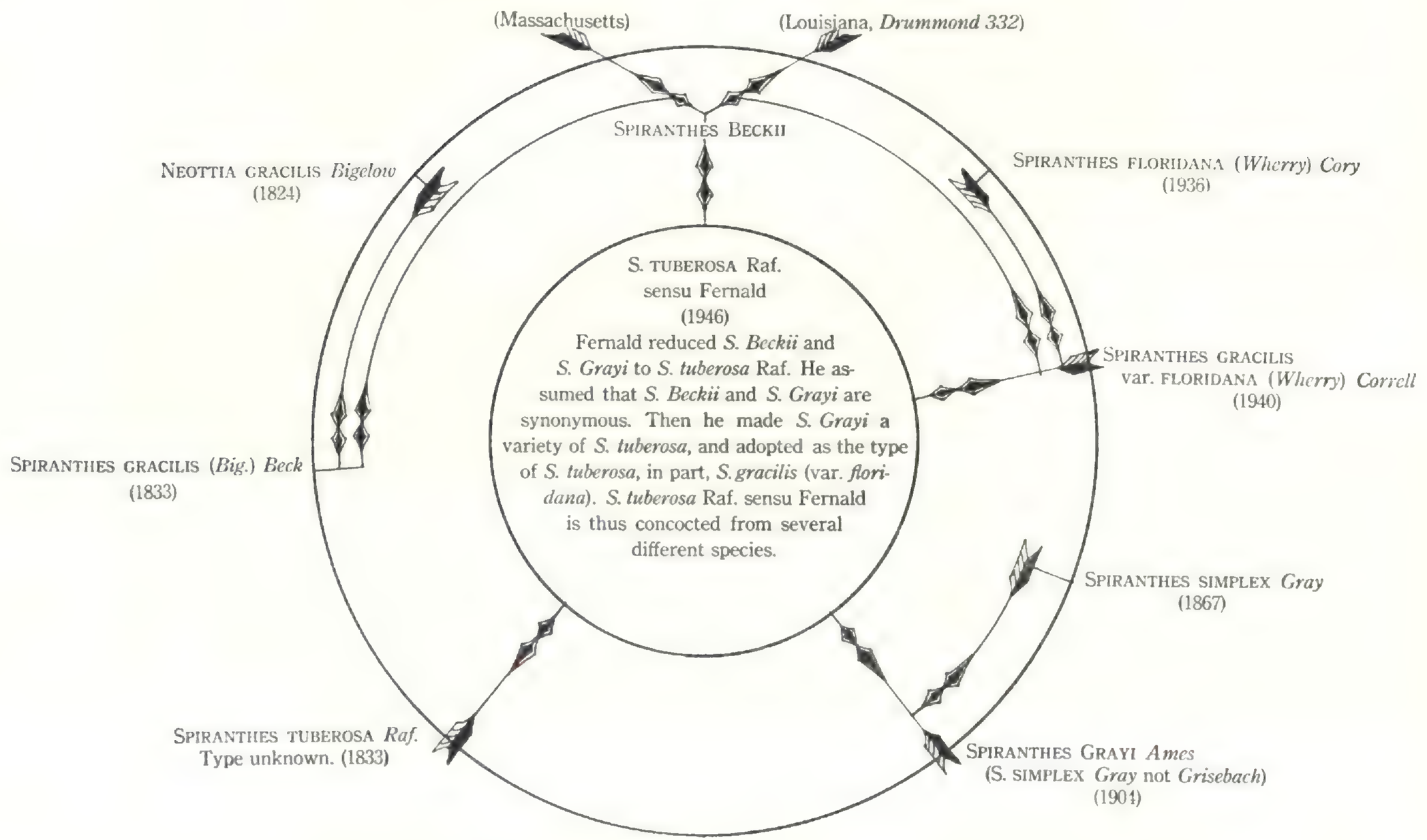
[3] Rhodora 48 (1946) 192.

tuberosa, as he interpreted it, consists of two strongly marked geographic variations. He stated that essentially all the material from New England belonged to one category, readily recognizable by the relatively close spikes of closely spiralling, often crowded flowers, and a thick, usually solitary vertical "tuber." To the other category he assigned all the material in the Gray Herbarium from eastern Texas to Florida and north to South Carolina in which the spikes are strongly secund without or with few spiral twists in the rachis and with the relatively few flowers distant and not overlapping. Fernald stated further: "From North Carolina to New Jersey both variations, with some transitions, occur, the plant often reaching a height of 5.25 dm., while its roots are usually more slender and not infrequently 2 or even 3. This is true *S. tuberosa* Raf. . . ." It is difficult to see why *S. tuberosa*, described by Rafinesque as "rad. tuberosa monorchis" should be applied to the southern variant with not infrequently 2 or even 3 roots, rather than to the northern one with its characteristic thick solitary turbinate root.

In his recent articles on Spiranthes, Professor Fernald has placed stress on the structure or aspect of the spikes and on the presence or absence of foliage at flowering time, seeming to regard vegetative characters as reliable guides to specific differences in the genus. Whether the spikes are congested or slender; whether they are composed of many spirals or of few; whether the flowers are quaquaversal or secund is a manifestation of the nature of seasonal growth. The behavior of the flowers in the spikes in their response to torsion does not give rise to a fixed specific or inherited pattern. As should be expected, rachidial torsion varies in intensity from plant to plant, and in the same species varying degrees of spirality in the arrangement of the flowers may be regarded

as the consequence of individual variation or as the effects of climate or environment. Under certain climatic conditions and in response to favorable edaphic influences the flower scape may elongate rapidly. Torsion in the rachis then becomes so regulated that secund flowers with closely imbricating bracts are the rule rather than the exception (cf. Plate III, fig. 3). If floral development is hastened by climatic conditions, the period of anthesis coincides with the maturing of the foliage. In Florida, where the spring approaches with a rush and vegetation becomes suddenly active, *S. gracilis* var. *floridana* has its commonly secund flowers fully open before the leaves have had time to attain maturity. This happens also in the northern area of distribution for the species. It would be a very simple matter to pick out dried specimens of *S. gracilis* from Nova Scotia and dried specimens of var. *floridana* from Florida which would be so alike in floral and vegetative aspects that even expert botanists, without helpful labels to assist them, would be unable to tell these variants apart.

It would seem that in his treatment of *Spiranthes tuberosa* Raf. Professor Fernald has added measurably to the "muddle" he attributed to Lindley, inasmuch as *S. tuberosa* Raf., *sensu* Fernald (like *S. Beckii* Lindl.) is "concocted from elements of several different species." In view of the difficulty experienced in properly applying the name *S. tuberosa* Raf., without a type specimen to guide us, it would seem preferable to abandon it, and to use *S. Grayi* Ames and *S. gracilis* (Bigel.) Beck var. *floridana* (Wherry) Correll for the two elements involved.


SPIRANTHES BECKII *Lindl.* (1840)
This species was composed of two distinct units, one from Massachusetts, one from Louisiana (both units referable to *S. gracilis* (Big.) Beck).
(Massachusetts)
(Louisiana, *Drummond 332*)
SPIRANTHES BECKII
NEOTTIA GRACILIS *Bigelow* (1824)
SPIRANTHES FLORIDANA (*Wherry*) *Cory* (1936)
S. TUBEROSA Raf. sensu Fernald (1946)
Fernald reduced *S. Beckii* and *S. Grayi* to *S. tuberosa* Raf. He assumed that *S. Beckii* and *S. Grayi* are synonymous. Then he made *S. Grayi* a variety of *S. tuberosa*, and adopted as the type of *S. tuberosa*, in part, *S. gracilis* (var. *floridana*). *S. tuberosa* Raf. sensu Fernald is thus concocted from several different species.
SPIRANTHES GRACILIS var. FLORIDANA (*Wherry*) *Correll* (1940)
SPIRANTHES GRACILIS (*Big.*) *Beck* (1833)
SPIRANTHES SIMPLEX *Gray* (1867)
SPIRANTHES TUBEROSA *Raf.* Type unknown. (1833)
SPIRANTHES GRAYI *Ames* (S. SIMPLEX *Gray* not *Grisebach*) (1904)

EXPLANATION OF THE ILLUSTRATION

PLATE II. SPIRANTHES GRAYI *Ames.* 1, lip from a Massachusetts specimen, 3 mm. long, 2.5 mm. wide. 2, lip, from a Georgia specimen, 3.5 mm. long, 2.5 mm. wide.

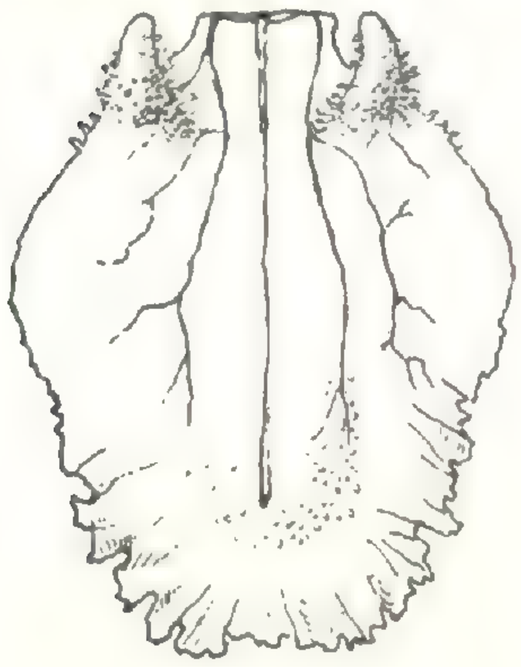
SPIRANTHES GRACILIS VAR. FLORIDANA (*Wherry*) *Correll.* 3, lip from *Drummond 332* (from a camera-lucida sketch by Victor S. Summerhayes), 3.4 mm. long, 1.3 mm. wide. 5, lip from a Floridian specimen (Volusia County), 4.5 mm. long, 1.5 mm. wide.

SPIRANTHES GRACILIS (*Bigelow*) *Beck.* 4, lip from a Canadian specimen, 5 mm. long, 2.5 mm. wide. 6, lip from a Massachusetts specimen, 5 mm. long, 2.5 mm. wide.

Figs. 1, 2, 4, 5 & 6 drawn by BLANCHE AMES, *with the aid of the camera-lucida.*

PLATE II

Spiranthes Grayi
Massachusetts

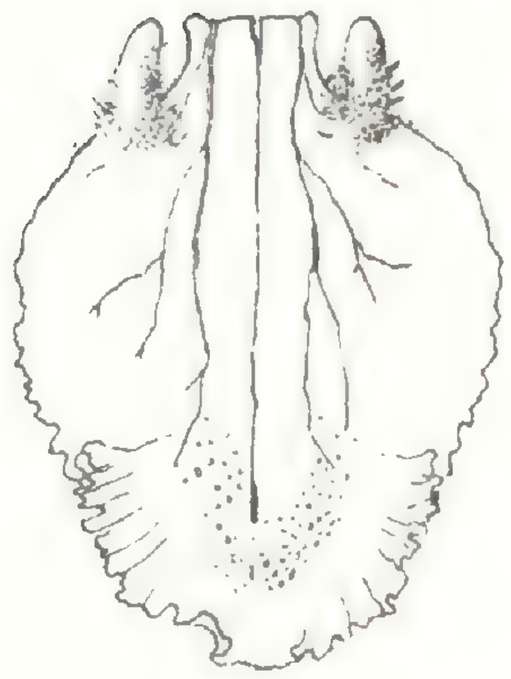


1

Spiranthes gracilis
var. floridana

3

Spiranthes Grayi
Georgia

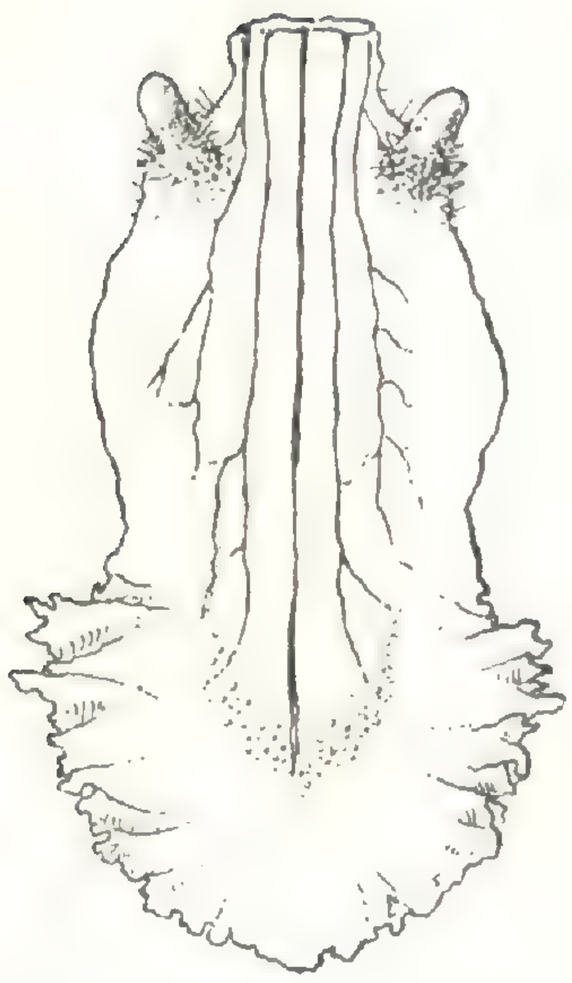


2

New Orleans, Drummond 332.

Camera lucida
V. S. S.
Sept. 1947.

4

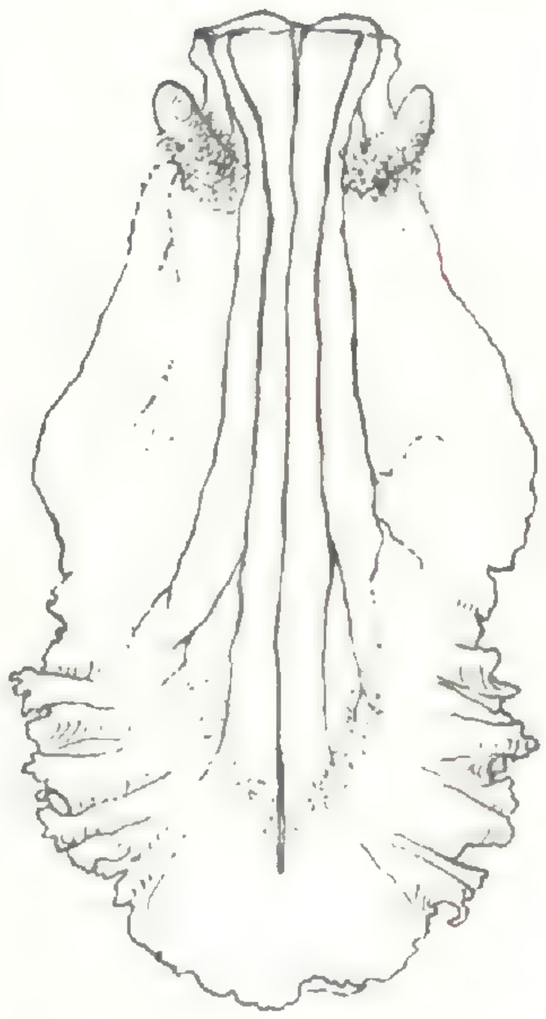


Canada

5

Var. floridana

6



Massachusetts

Spiranthes gracilis (Big.) Beck

II. Spiranthes gracilis var. floridana

Spiranthes gracilis (*Bigel.*) *Beck* var. **floridana** (*Wherry*) *Correll* in Bot. Mus. Leafl. Harv. Univ. 8 (1940) 76.

Spiranthes Beckii Lindley Gen. & Sp. Orch. Pl. (1840) 472, *ex parte*.

Ibidium floridanum Wherry in Journ. Wash. Acad. 21 (1931) 49.

Spiranthes floridana (Wherry) Cory in Rhodora 38 (1936) 405.

Spiranthes floridana (Wherry) Correll in Journ. Elisha Mitchell Sci. Soc. 53 (1937) 159.

Spiranthes tuberosa Rafinesque, *sensu* Fernald in Rhodora 48 (1946) 10, 189.

When Edgar T. Wherry described *Ibidium floridanum*, he cited *Spiranthes gracilis* (Bigel.) Beck as a close ally, admitting that a search for morphological differences between these species had not been wholly successful. The only differences of consequence between *Ibidium floridanum* and its northern ally are, as Wherry stated, chiefly in the color of the flowers, the dates of anthesis and the geographical distribution. It should be noted that Wherry used the length of the lateral sepals in relation to "the bend of the lip" as a separative character, but this does not appear to be a dependable guide to a constant difference between the northern and southern representatives of the *Spiranthes gracilis* alliance. Wherry gave the geographical distribution of *Ibidium floridanum* as reaching westward to Texas and northward to South Carolina, with a blooming season extending from December to May. He reported specimens from South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana and Texas. For *Spiranthes gracilis* (Bigel.) Beck he gave

Aiken County, South Carolina, Alabama and Arkansas as the southernmost boundary, with a blooming season extending from July to September.

When growing wild, *Spiranthes gracilis* var. *floridana* may be recognized by the yellowish hue of the rachis and floral bracts and in having the central part of the lip yellow rather than green as in *S. gracilis*. The lip is variable in outline and length, ranging from 3–5 mm. long and varying from pandurate to narrowly oblong, the apical portion being conspicuously denticulate and variously fluted on the margin.

The variety exhibits greater variation than the species, ranging from 1–4 dm. or more in height, with the flowers 3–5 mm. long. The flowers in their arrangement vary from quaquaversal to secund. As is true of the typical species in the extreme North, flowers and leaves are usually present simultaneously. In their venation and texture the leaves of specimens from Florida, Canada and New England are very much alike and arouse the suspicion that the differences in foliar texture between variants of *S. gracilis* emphasized by Professor Fernald in "Rhodora" (48 (1946) 8, t. 993, fig. 6; 994, fig. 5) are the exception rather than the rule and are surely not of taxonomic significance.

Wherry gave the date of the earliest record for the discovery of the variety as 1834, depending on specimens collected by Burrows at Tampa Bay, Florida. In establishing this record he overlooked Drummond's specimens (no. 332) (a component of *Spiranthes Beckii* Lindl.) from New Orleans, collected in 1832.

Until 1905, *S. gracilis* var. *floridana* remained one of the rarest of our Spiranthes. In that year, collecting for me in Dade and Lee Counties, Florida, A. A. Eaton found an abundance of specimens, blooming in February and March. After prolonged study, during which two

"herbarium names" came into being, one honoring Eaton, I concluded that the Floridian Spiranthes was puzzlingly close to *S. gracilis* and at most simply a geographical variety.

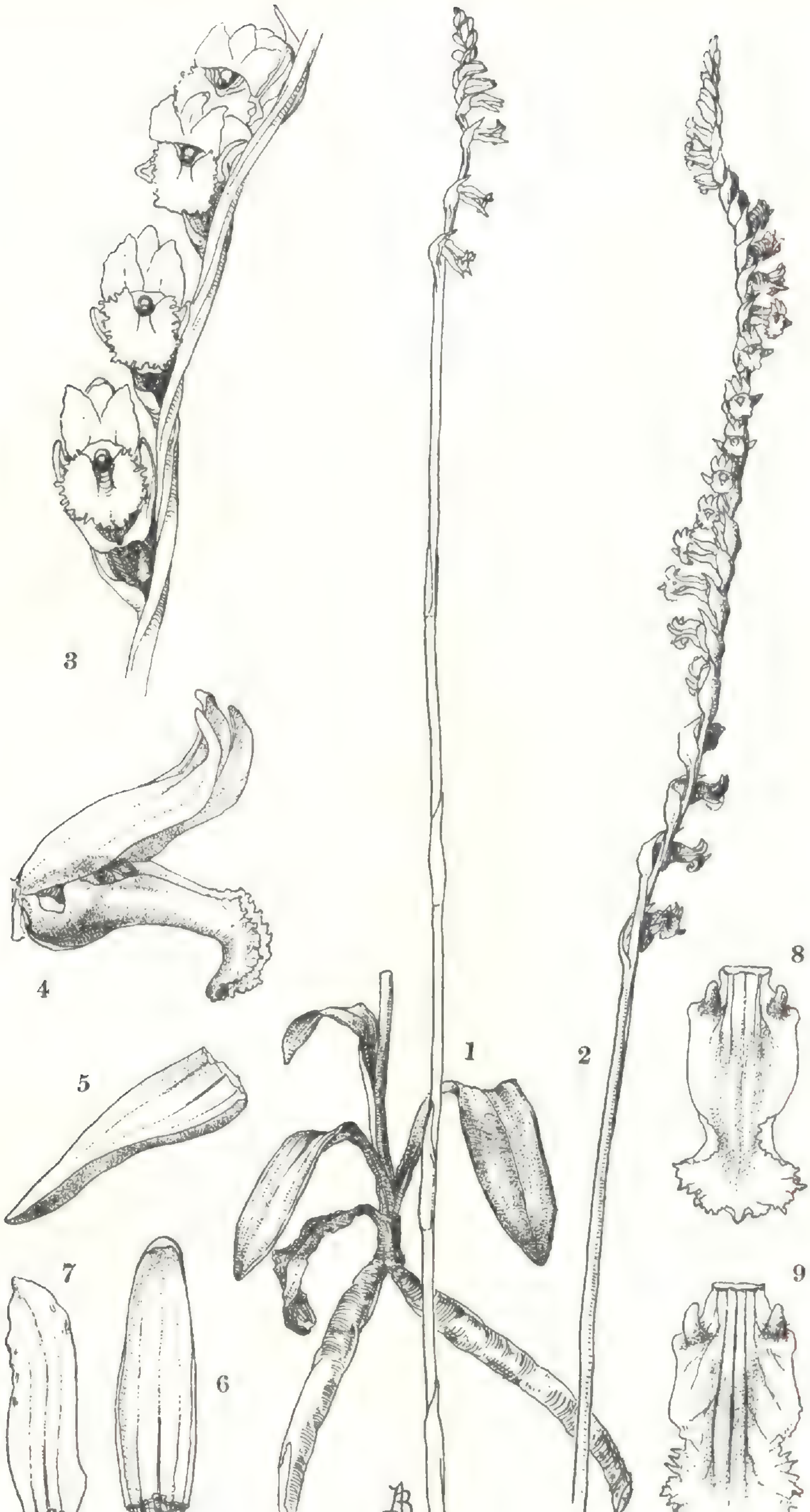
It may well be that morphological differences sustaining Wherry's conclusions may be discovered, but as yet I have not found them. However, it is indeed clear, that the Floridian variant is much more puzzling taxonomically than the Canadian one which Fernald has separated out because the flowers are usually secund and the leaves are present during anthesis.

EXPLANATION OF THE ILLUSTRATION

PLATE III. SPIRANTHES GRACILIS VAR. FLORIDANA (*Wherry*) *Correll*. 1, plant, natural size, from Volusia County, Florida, February 4, 1947. 2, spike, natural size, from Volusia County, Florida, March, 1944. 3, part of spike enlarged to illustrate rachidial torsion and its effect on the arrangement of secund flowers. 4, flower, side view (lateral sepals removed), about eight times natural size. 5, a lateral sepal, about six times natural size. 6, dorsal sepal, about six times natural size. 7, a petal about six times natural size. 8, lip, partly spread out, about six times natural size. 9, lip, flattened to show contour, about six times natural size.

Drawn from fresh specimens with the aid of the camera-lucida, by BLANCHE AMES.

Plate III



BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, DECEMBER 29, 1947 VOL. 13, NO. 3

CHICHA, A NATIVE SOUTH AMERICAN BEER

BY

HUGH C. CUTLER[1] AND MARTIN CARDENAS[2]

SIMPLE FERMENTED beverages enlivened the ceremonies of most Indian groups in the Americas long before the Conquest. These mildly alcoholic brews were so common in some regions that they may be regarded as furnishing substantial contributions to the diet. Even today this is true of Central Mexico, where pulque, made from the sap of the maguey plant, is the national drink; and of much of Bolivia and Peru, where enormous quantities of maize chicha are consumed.

When discussing chicha it is necessary to specify the type, for the word "chicha" was spread by the Spaniards so that it is now used to designate both alcoholic and non-alcoholic beverages made from a wide variety of plants and prepared in diverse fashions. Many of these are listed by La Barre (1938). In a relatively simple community of the civilized Takana Indians near Rurrenabaque in the Bolivian lowlands, intoxicating chicha is prepared from mandioca (*Manihot esculenta* Crantz,

[1] Formerly Research Associate of the Botanical Museum of Harvard University. This work is part of that done while a Fellow of the Guggenheim Foundation, 1946–47.

[2] Professor of Plant Pathology and Genetics, Universidad Autonoma "Simon Bolivar," Cochabamba, Bolivia.

called *e mi he*[3] in Takana), from ripe plantains (*na sa puri*), from fruits of the wine palm (*bi*, a species of *Mauritia*), from flour corn (*di he dure*), and from flint corn (*di he tada*). There are also non-alcoholic chichas made from toasted corn flour or from ground toasted peanuts, the latter probably having been introduced into Rurrenabaque from the southeast.

In the highlands and valleys of Bolivia there are two non-alcoholic beverages called chicha. *Chicha de quinoa*, or *aloja*, is usually merely water in which quinoa (*Chenopodium Quinoa* Willd.) has been boiled. Sometimes sugar and cinnamon are added. For *chicha de maní*, or *tecti* in the Aymara language, peanuts are toasted and ground, then toasted again to remove the oil. Whenever peanut chicha is to be made some peanut paste and sugar are stirred into quinoa chicha and peanut oil is poured over the surface. Sweetened drinks made of toasted and ground maize or barley are usually called *tostado*, although they are occasionally called chicha.

A simple alcoholic chicha can be made by mixing a substance containing starch or sugar with water and allowing the liquid to ferment. However, very little chicha is prepared in this way. Most chicha is made by methods which increase the alcoholic content and improve the flavor, the increase in alcoholic content being brought about by converting some of the starches to sugars which are more readily available for fermentation. An enzyme, diastase, will bring about this change, and in South America the most common source of diastase for chicha-making is saliva. The custom of masticating roots, fruits and grains in the preparation of beverages is widespread. Explorers have found chicha made in this fashion among

[3] Native words are spelled in the fashion of the literate population of the area in which they occur. Pronunciation and accent follow the usual rules for Spanish.

the most primitive as well as among some of the more advanced tribes. The raw materials chewed for fermented beverages have been reported to be mandioca in lowland Ecuador (Flornoy, 1945); mandioca and maize in central Brazil (Roquette-Pinto, 1938); maize and sweet potatoes in coastal Brazil (Métraux and Nimuendajú, 1946); algarroba (*Prosopis* spp.), tusca (*Acacia aroma* Gill.) and chanar fruits (*Gourlcia spinosa* (Mol.) Skeels) in the Chaco of Bolivia, Paraguay and Argentina near the Pilcomayo River (Métraux, 1946); and maize in the highlands of Peru (Zárate, 1853).

Malting (soaking grain in water and then allowing it to germinate) is another method of introducing diastase. Garcilaso de la Vega[4] (1800), José de Acosta (1940), Bernabé Cobo (1890-1893) and Hipólito Ruíz (1931) briefly mention malting. The early writers did not give detailed information on native foods and were generally scornful of indigenous customs. They left no complete account of chicha-making. It is probable, however, that malting is a pre-Columbian development.

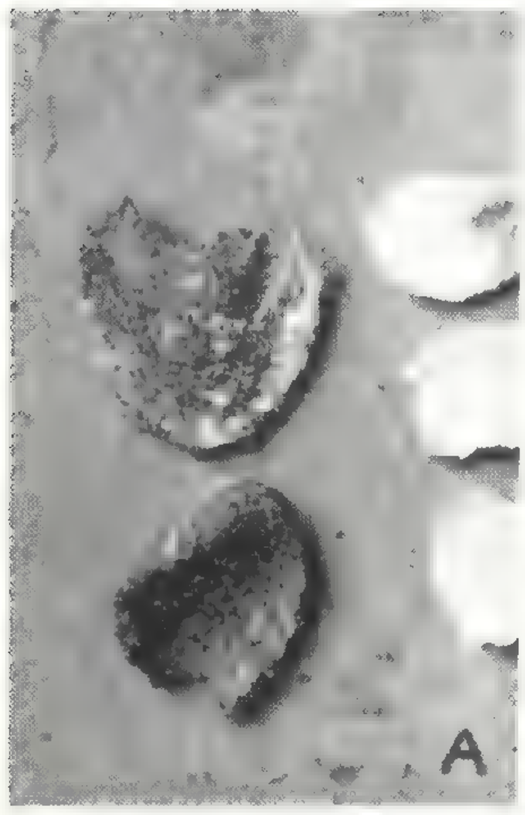
Malting is common in most of Bolivia and Peru, especially in the highlands, but it is not common in other regions. It is probable that maize and quinoa were first domesticated in Bolivia and Peru, and mandioca in east-central Brazil. The roots of mandioca could not be malted, but they are very well suited to mastication. Where seed crops had been cultivated for a long time there would have been ample opportunity to develop malting and still continue the chewing methods which had been found to be adapted to the pods of algarroba and similar uncultivated raw materials.

[4]The dates given are those of the editions consulted, and are not the dates when written, nor necessarily the dates of the respective first editions. The references to Acosta and Cobo were suggested by Dr. John Rowe.

EXPLANATION OF THE ILLUSTRATION

PLATE IV. A. Salivated corn flour or *muko*. (Left) from *culli* maize; (right) from *huilcaparu*. B. Interior of a chicha-making establishment in Punata, Bolivia. The steaming pan over the fire is the *perol*. The large containers are *wirkis*, for the temporary storage of chicha materials while being processed. C. Salivating maize flour or *mukeando*. Punata, Bolivia. D. *Cantaros* in which chicha is placed near the end of the process. The chicha is sold directly from these jars. Cochabamba.

Plate IV



The authors have studied chicha-making in Bolivia at Tiquipaya, Quillacollo, Punata, Sacaba and Cochabamba among the Quecha-white population. We were able to secure little information of value from the civilized Chiquitano Indians of Santiago de Chiquitos, but from other lowland groups, particularly the Reyesanos near Reyes and the Takanas between Reyes and Tumapasa, we secured quite complete data. The literature on the subject was of very little help except to confirm our observation that chicha-making is an old art, widespread in South America.

Chicha-making in the Cochabamba Valley

Because the chicha-making methods in use in the Cochabamba Valley, located at an altitude of more than eight thousand feet in the Bolivian highlands, are the most complex, and because they are undergoing changes, they will be considered in greater detail than the methods employed by the lowland Indians.

The valleys of Bolivia are separated by high mountain ranges, and inter-valley commerce was long restricted by both physiographic and ethnic barriers. The consequent existence of many small centers of cultivated plant populations which had only an occasional interchange of plant material constitutes an ideal situation for the rapid evolution of numerous forms of plants. In the Cochabamba Valley, for example, there are many varieties of maize, some with highly specialized uses (Cutler, 1946).

Raw Materials

In Cochabamba, chicha is prepared from maize. The berries of molle (*Schinus Molle* L.) and the chewed pods of algarroba are no longer utilized. At slightly higher elevations an alcoholic chicha is sometimes made from malted quinoa grains.

The most highly preferred maize for chicha is *chuspillo*, a many-rowed sweet corn. Most of this sweet corn is grown on the larger haciendas for use only as toasted grains, or for the preparation of an especially strong chicha.

The next choice for chicha is *culli*, a cherry-red to almost black maize which contains large amounts of water-soluble anthocyanins. Usually the purple cobs are ground and added to the corn flour. Chicha made from *culli* is a rich Burgundy color. Occasionally the fruits of one of the various Opuntias called *airampu* (*Opuntia sulphurea* G. Don in the Cochabamba district (Pl. IVc), *O. Sochrensii* Britt. & Rose near La Paz, and an undescribed species from near Arani) are added to chicha to give it this desired color. The young inflorescences of a purple amaranth are also said to be used to dye chicha.

Uchukilla, a maize with small ears closely resembling *culli* except that it is white, is the third choice for chicha-making in the Cochabamba Valley. Very similar small orange flint ears grown at altitudes of about 2,700 meters are used for chicha in Totora, in the Department of Cochabamba. The chicha made from this maize is one of the best.

Another preferred source of chicha is *paltal hualtacu*, also somewhat like *uchukilla* but with larger ears, yellow flint endosperm and an occasional slight tinge of blue in the aleurone.

Notwithstanding the fact that chicha made from any of the five types of maize already referred to is of superior quality, the most common source of the beverage in the Cochabamba Valley is *huilcapara* the maize most frequently grown. This has a rust-red cob with fourteen to eighteen rows of dented grains. The denting varies from small dimples to as much as is found in the most extreme of North American dents. The endosperm is yellow and

the aleurone is a deeper blue than that of *paltal hualtacu*. This combination makes the grains appear brownish, with a silvery sheen produced by minute air spaces under the pericarp.

Forbes (1870, p. 249) says, "In some parts a fermented drink is made by the Indians from the sweet stalk of the young green Indian corn, called "huiru" (wiru): this is the name of the stalk." Although sweet young stalks, usually of *culli* or *uchukilla*, are sold today in the markets to be chewed like sugar cane, they are not used in chicha-making.

Preliminary Steps

The maize grains are usually ground by hand, often with a half-moon-shaped stone rocker (*maran uña*) on a flat stone (*maran*) as has been done for centuries. The flour is then mixed with saliva. On some of the larger haciendas it is still the custom to have women and children gather in groups to do this (Pl. IVc). The flour is moistened very slightly with water, rolled into a ball of convenient size and popped into the mouth. It is thoroughly worked with the tongue until well mixed with saliva, after which it is pressed against the roof of the mouth to form a single mass, then shoved forward with the tongue and removed with the fingers. The teeth play very little part in the process. For this reason we prefer the term "salivation," and use the word "mastication" only when referring to cases where it is necessary for the teeth to macerate the raw materials, as is done when algarroba, mandioca or sweet potatoes are used.

The salivated morsels are dried in the sun and sacked for storage and shipment. They roughly resemble sets of false upper teeth (Pl. IVA). Since *muko*, as the salivated flour is called, commands a much higher price than unsalivated flour, property owners try to convert as much flour as possible into *muko*.

EXPLANATION OF THE ILLUSTRATION

PLATE V. A. Grinding corn flour, Punata, Bolivia. B. Chicha sign near Cochabamba. C. Chicha sign in Tiquipaya.

Plate V

In some places in the Cochabamba Valley maize is malted. In Tiquipaya this is done by soaking the grains overnight in a pottery jar with enough water to cover them. The next day the grains are spread to a depth of about four inches on some leaves, and covered with several blankets. The germinating seedlings generate considerable heat. The temperature in one such bed was 34°C. When the shoots are nearly as long as the grains they are placed in the sun to dry. In Tiquipaya, and also in Cuzco, Peru, it is a common sight to see these sprouted grains spread out on bright colored blankets in the dusty streets. When dry, the malted grains are ground. Both the germinating grain and the flour prepared from it are called *huiñapu*.

Brewing

The First Day

A wide-mouthed earthen pot (*wirki*) is filled about one third full with dried and ground malted grains (*huiñapu*) or salivated flour (*muko*). When *muko* is used, unsalivated maize flour is often mixed with it. Crude sugar (*chancaca*), or the pulp of a squash (*Cucurbita ficifolia* Bouché) known as *layacote*, is occasionally added. The pot, which is about thirty inches high and thirty-four inches in diameter, is filled with water heated to about 75°C. Boiling water is not used as it is said to produce an undesirable pasty consistency. After being well mixed for nearly an hour the mixture is allowed to settle and cool further. Three layers can then be distinguished: a liquid (*upi*) above; an almost jelly-like layer in the middle; and coarser particles (*hanchi*) below. The cloudy liquid *upi* is scooped up with a gourd (either *Crescentia Cujete* L., known in the Quecha language as *tutuma;* or *Lagenaria siceraria* (Mol.) Standl., known as *mate*) and placed in another large-mouthed pot and allowed to

stand. The middle layer is transferred to a large shallow pan (*perol*) permanently installed on a clay support over a fire (Pl. IVB). During the last few hours of the day this second layer simmers and concentrates. To the *hanchi* may be added more *muko* or some roughly broken corn (*tiki*) and more hot water. Rarely quinoa is added instead of the *tiki*. This mixture is agitated again, allowed to settle, and the liquid portion is then added to the original *upi*.

The Second Day

The *upi* continues to stand. The fire under the *perol* is rebuilt and the mixture is allowed to simmer for several hours longer until it becomes caramel-like in color and flavor. This product, called *misqui kketa*, is transferred to a *zeirki* and allowed to cool. Most of the by-products of chicha-making are no longer important since their place has been taken by sweets which are more easily made with sugar. A small amount of the *misqui kketa* may be eaten in the home where the chicha is being prepared, but nearly all of it is used in the chicha itself. It is probable that the *misqui kketa* was originally used solely as a sweet and was not added to the chicha. Chicha-makers, like alchemists of old, surround their art with an aura of mystery, and probably emphasize some of their steps in such a way as to confound inquisitive consumers.

The *hanchi* left in the bottom of the original open-mouthed *zeirki* is drained of its remaining moisture in the following manner: A cylinder woven of splints is pressed vertically into the layer of *hanchi*. The particles inside the cylinder are removed and packed about the periphery. The last remnant of liquid filters through the woven cylinder. This is a sweet, clear, non-alcoholic liquid called *chua conchu* which may be drunk in the

house where the chicha is made, but, more commonly, is added to the *upi*. The further disposition of the *hanchi* will be discussed later.

The Third Day

The *upi*, which is now slightly bitter, is transferred to the *perol*, the large shallow pan over a fire. A thick white sediment remains in the *wirki*. This sediment, known as *upi alpi*, is further treated by adding sugar, cinnamon and some orange leaves and then boiling. It is then eaten as a delicacy in the household where the chicha is being produced.

After the *upi* has boiled for about three hours in the *perol* it is transferred to a *wirki* to cool. In Cochabamba, which is 2,572 meters above sea level, boiling occurs at 89°C. At the end of this third day the *misqui kketa* is added to the *upi*, an operation locally called *kketacha*.

The Fourth Day

The mixture of *upi* and *misqui kketa* has now begun to ferment and bubbles violently. This action soon slows down and the liquid is transferred to narrower-mouthed pots (*centaros*) at the place where the chicha will be sold or consumed (Pl. IVD).

The Fifth to the Tenth Day

In the Cochabamba Valley, very few bubbles arise and fermentation is considered to be complete after about six days. At higher and cooler altitudes more days are needed, while in the hot lowlands less than two days may suffice.

Before the chicha is drunk, the floating froth (*aca ñahui*) is removed with the cupped hand. This froth contains oil, much yeast and some extraneous material. It is used as a sort of French polish for furniture. Occasionally

EXPLANATION OF THE ILLUSTRATION

PLATE VI. Chicha signs. A. Sacaba. B. Arani. C. Calla-Calla. D. Cochabamba. E. Taquina. F. Cochabamba.

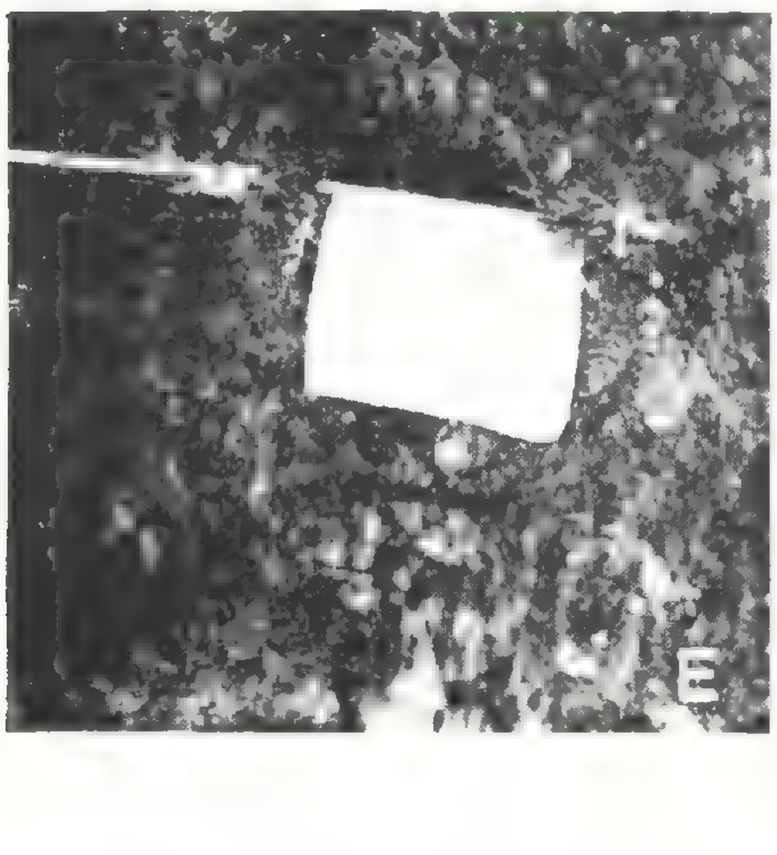
Plate VI

A

B

C

D


E

F

chicha-makers may add some of this yeasty mixture to new batches of green chicha as a starter. Usually, however, this is unnecessary because the porous earthen jars are only slightly washed out and so are normally well supplied with yeast. The jars are washed with ashes and water, swished about with a branch of molle (*Schinus Molle* L.) or *huai cha* (*Senecio clivicolus* Wedd.).

After the chicha has been drunk, a layer of sediment remains in the bottom of the pot. This sediment, the *borra de chicha*, is laid on a gunny-sack stretched over a small jar. A liquid, the *sutu*, which resembles chicha in color, but lacks the carbonated sparkle and cidery tang of good chicha, drips through the sacking. *Sutu* is greatly prized for it is reputed to have a higher alcoholic content than chicha. It is usually consumed at home, sweetened with sugar and dyed a wine-color with *airampu* (see p. 40). For each forty liters of chicha only about one liter of *sutu* is obtained. After the *sutu* is drained off, the remaining *borra* is fed to pigs and chickens, or is saved to be used in making a weak chicha to be discussed below. It may also be added to bread dough, for it provides yeast as well as filler.

At the end of the second day of chicha-making a coarse sediment, the *hanchi*, remains. This is often given to pigs and chickens, but it may also be used to make *kaima*, a cheap and weak chicha. Cold water is mixed with the *hanchi* and it is allowed to stand. After a short time a sediment settles to the bottom. The upper part of this sediment is smooth and creamy. This *kketa ordinaria*, as it is called, may be cooked with brown sugar to make a custard, or it may be added to the *misqui kketa* when it is being concentrated. If *kketa ordinaria* is added to the *misqui kketa*, more *borra* is left after the chicha has been drunk. The coarser, lower part of the sediment is fed to pigs. The supernatant liquid (*seke*) is removed and boiled

in the *perol* for two hours, then transferred to a tall pot (*cantaro*) and allowed to stand for two or three days. *Borra*, usually from a previous lot of chicha, is then added. The beverage thus produced is called *kaima*. It is consumed mainly by the Indian field laborers whose work in the hot sun makes them particularly susceptible to alcohol. They prefer *kaima* to the stronger chicha because it is possible to drink more without becoming drunk or sleepy. The sediment of the *kaima*, also called *hanchi*, is fed to pigs.

Consumption and Marketing

Well-made chicha is an attractive drink, clear and sparkling, with a flavor somewhat similar to that of apple cider. Its alcoholic content varies greatly, from about two per cent in new or in weak and watered chicha to as high as twelve per cent in a few exceptional samples. Most Cochabamba chicha has five per cent alcohol or less.

When chicha is ready for sale, a sign, the *aca llantu* ("Chicha flag") is displayed. *Llantu* is probably related to *llaitu*, the word for a fringe which denotes nobility or rulership. The frequent occurrence of fringes and tassels in chicha signs suggests that there may be some basis to the local belief that the better types of chicha were formerly reserved for the ruling class.

The simplest chicha signs are white flags attached to tall poles. These are seen only in the country districts. During fiestas the flags are decorated with flowers and colored ribbons (Pl. VIE). Some of the signs in small settlements are very ornate. Fancy tin stars, wooden condors, reed boats, cloth squares, tissue-paper frills and wooden plaques are common. Some of these are shown in Plates V and VI. In Quillacollo and Cochabamba there are laws which prohibit these fancy devices, and

most signs are simple lettered boards. These usually announce "Chicha," "Buena Chicha" (Good Chicha), "Chicha Pumateña" (Chicha from Punata) or "Chicha Clizeña (Chicha from Clissa). Many *chicherias* also have a parrot in the doorway so that the illiterate may know where to drink. One *chicheria* places a single parrot in the doorway when ordinary chicha is for sale, but two parrots when the chicha is exceptionally good.

Chicha is taxed in Bolivia. Each year the right to collect these taxes is auctioned to the highest bidder. The tax is 48 Bolivian centavos (about one cent in United States money) for each bottle of 660 c.c. A bottle of chicha is usually sold for about eight United States cents. The tax is collected when the chicha is made. In Cochabamba and its suburbs, with a population of about 80,000, according to the records of the Treasury of Cochabamba, taxes were paid in 1946 by 768 licensed *chicherias* on 4,617,388 liters of chicha. It is rumored that more than twice this amount was actually made.

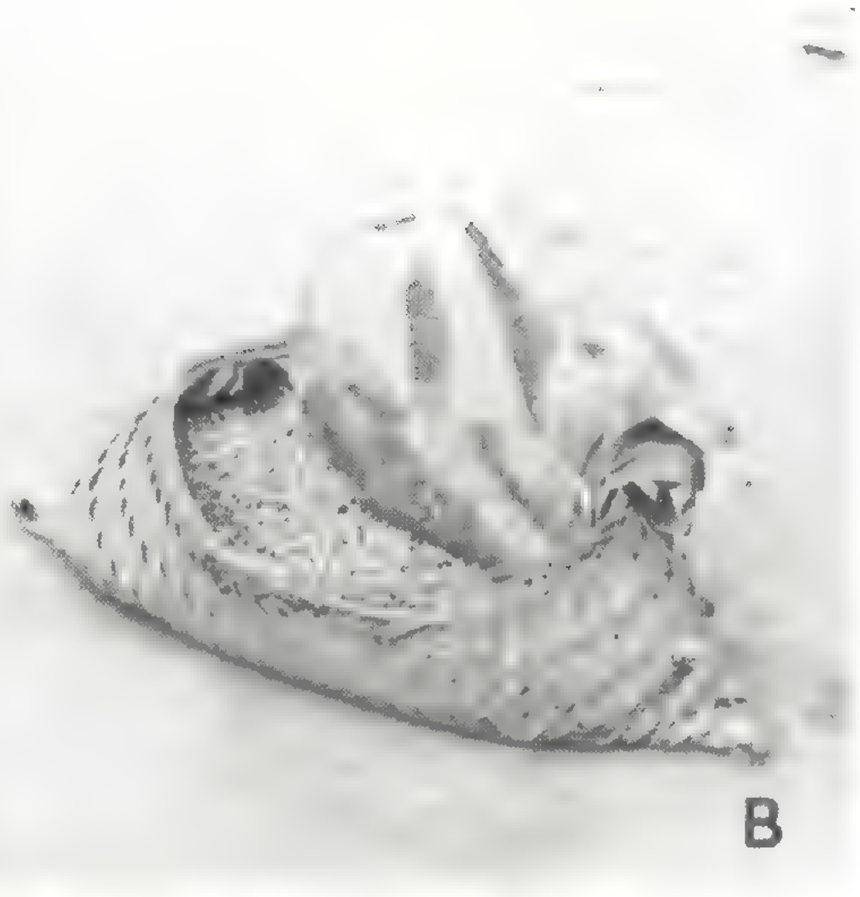
Chicha-making in the Bolivian Lowlands

Chicha-making in the Bolivian lowlands is a short and simple process. Since fermentation progresses rapidly in the tropical heat, and since the natives have only a few small pots, there is neither equipment nor time for the elaborate methods which prevail in the highland valleys. Among the Takana Indians who live on both sides of the Río Beni near Rurrenabaque, chicha forms a part of the daily food of most families and nearly all homes constantly have some in preparation. Métraux (1942, p. 42) states: "None of the Takana tribes is known to have brewed any fermented drink, ... a curious exception in an area where most tribes enjoyed several kinds of beer." We believe that fermented drinks have been known in this region for a long time, and were either

EXPLANATION OF THE ILLUSTRATION

PLATE VII. A. Grinding flour corn for chicha near Balas, Río Beni, Bolivia. B. Germinating corn grains for chicha, near Reyes, Bolivia. C. *Airampu* (*Opuntia sulphurea*). The seeds are used to dye chicha, near Cochabamba. D. Pounding grains of white flint corn for *somó* or *tuhuré*, Rurrenabaque, Bolivia.

Plate VII



not seen or not recorded by Métraux's sources of information.[5]

Most chicha is made from the long ears of dull orange flour corn. White flint maize is seldom used. The ears are kept in the husks, tied in pairs and hung over a pole on the rafters or under the trees until needed. A pointed wooden peg held in the hand is sometimes used to facilitate the removal of the husks and grains.

The grains are soaked overnight in a jar of water, then placed in a basket lined with Heliconia leaves and covered with more leaves (Pl. VIIB). Inside one basket the temperature was found to be 36°C. When the shoots are nearly as long as the seed (the sprouted grains are called *e bi data* in Takana), they are crushed with a rocker stone (*tumu*) on a semicircular hardwood board (*tada*) (Pl. VIIA). Usually some of this ground malted grain is salivated slightly by mixing it in the mouth. The malted, ground and salivated meal (*e be teni*) is immediately placed in a jar and mixed with warm water. The mixture is then boiled for three or four hours. The boiling liquid is called *e bi data du duki*, the liquid after boiling but still hot *sina métahi*, and the liquid when cold but not fermented *hui na métahi*. After it has cooled the liquid is strained (*da kwatai*) through a piece of cotton cloth and left in a narrow-mouthed jar to ferment (*patcha chenapúi*, i.e. to become strong). Although the chicha is at its best after two days, drinking usually begins soon after the liquid cools and before it has fermented, and continues until it is gone. After five days the chicha becomes vinegar-like, but it has usually been consumed

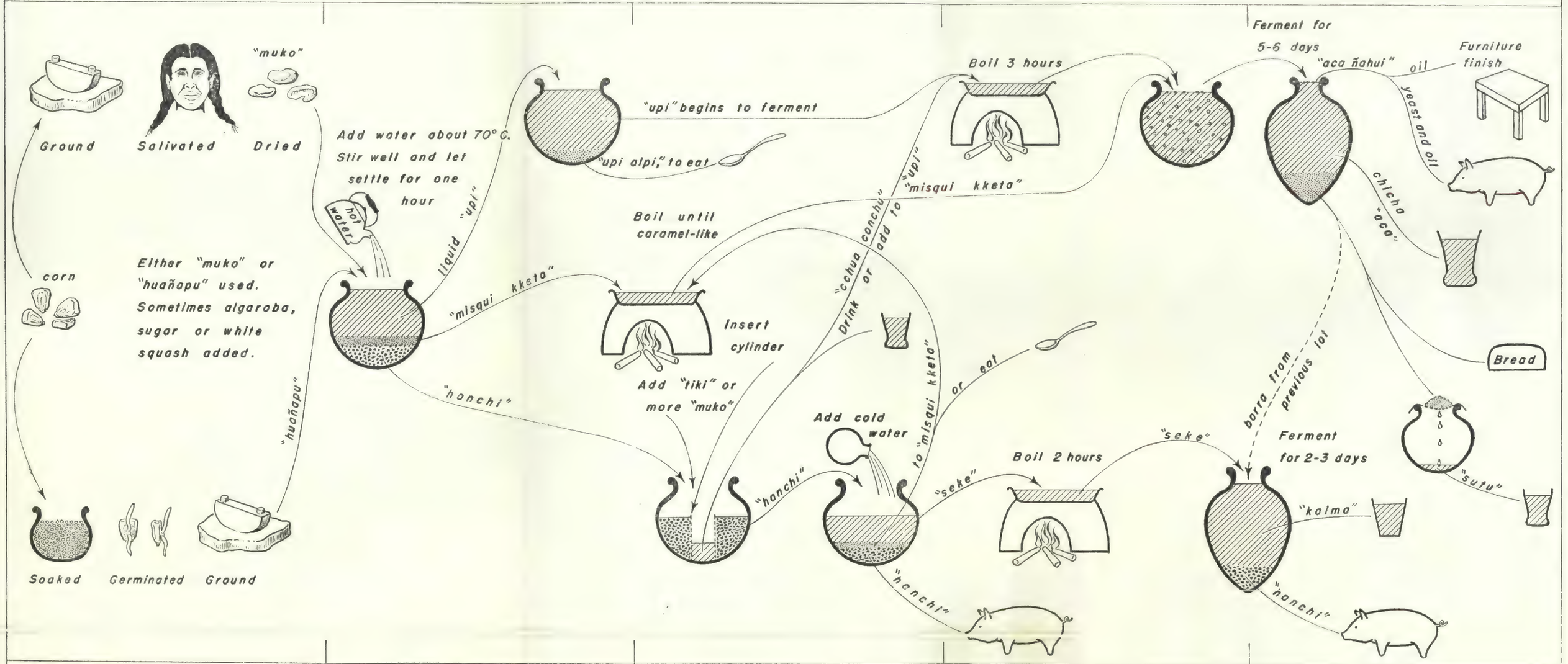
[5] The little that is known of the Takana language is summarized by Créqui-Montfort and Rivet (1921–22). Since they list only one word for chicha (*tupari*), we are including other Takana terms recorded near Rurrenabaque. These should be accepted with caution since they were recorded by one who is not a linguist and does not speak Takana.

before this. The sediment which was left after straining and that which remains in the pot after the chicha is drunk are thrown to the pigs and chickens. There are no by-products. Just as in the highlands no yeast is added. The liquid is boiled in one pot, however, and fermented in another which is merely rinsed out after each lot of chicha has been made.

White flint corn is used to make two drinks in the Río Beni town of Rurrenabaque. The grains are pounded in a wooden mortar (*taeú*) with a pestle (*mano taeú* in the Takana dialect of Rurrenabaque) to loosen the pericarp (Pl. VIIb). After winnowing, the grains are boiled in water for about three hours. Sugar is then added. When cool, this product is called *somó*, probably an introduced term. If allowed to ferment, it is called *tuhuré*.

Reference has been made to the sweet caramel-like paste (*misqui kketa*) produced in the highland chicha process. The Takana Indians prepare a similar sweet as the end-product in a process which is exactly like that for chicha up to the time of boiling. The malting, grinding and salivation have been completed and the water added. The mixture is then strained and boiled. However, instead of boiling for only a few hours, this process continues for almost a day until the liquid is sticky and caramel-like, and the Takana women judge it has reached its "point." This means that when cool it will harden just as properly made fudge does. While still hot the sticky liquid is poured or scraped onto the broad leaves of any one of several species of *Heliconia*. Usually it is eaten as a sweet (*eti hua;* in the Takana dialect spoken near Reyes, *e eua huara*). Since sugar cane is now common in the area, very few of the Takanas still make the sweet solely as a confection. It is usually utilized as an ingredient for a chicha prepared from the *bi* palm, a species of *Mauritia*.

STEPS IN THE MAKING OF CHICHA AND ITS BY-PRODUCTS IN THE COCHABAMBA VALLEY OF BOLIVIA



PRELIMINARIES | FIRST DAY | SECOND DAY | THIRD DAY | FOURTH TO TENTH DAYS

Drawn by Gordon W. Dillon

The fruits of this palm are boiled in water until the shell comes off. The mass is then worked with the hands and the corn sweet (*e ti hua*) added. This mixture is again boiled and broken up with the hands, after which it is strained through a sieve. After standing in pots for two days it is ready to be drunk. Natives claim that this chicha is stronger than that made from maize alone. Chicha made from the palm fruits alone without adding the corn sweet is weaker and is seldom prepared.

On the western margin of the Bolivian Chaco near Camiri and Lagunillas, the Chiriguano Indians make chicha by simply mixing boiled and masticated grains of maize with hot water and allowing this to ferment. In Santa Cruz, plain ground corn is sometimes mixed with hot water and left to ferment. This makes a weak chicha which must be consumed as soon as it has fermented. According to Métraux (1946), the Indians near the Pilcomayo River in the Chaco of Bolivia and Paraguay use the fruits of algarroba (*Prosopis* spp.), chanar (*Gourliea spinosa* (Mol.) Skeels), and tusca (*Acacia aroma* Gill.) in the preparation of alcoholic drinks. These fruits, particularly algarroba, are usually masticated as a preliminary step in the process.

These observations on the manufacture of chicha in Bolivia are presented as introductory material to a possible future study of native American beverages. A complete report on the manufacture and use of such beverages together with their associated ceremonies and superstitions would yield valuable information as to the spread of food plants and customs. Before such a study can be made, however, it will be necessary for the student to go into the field and collect his own data, since the information available in the literature, and even in the notebooks of ethnologists, will not suffice for more than the roughest of outlines.

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BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JULY 27, 1948 VOL. 13, NO. 4

VASCULAR ANATOMY OF ORCHID FLOWERS

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THAT the structural complexities of a flower can be made clear by a study of floral anatomy in relation to its vascularization is becoming a prevalent thought. While such a study is being concentrated on the members of several other natural orders, orchids, characterized by their "over-specialized" floral organization, still remain to be attacked from this angle.

Robert Brown (1831) was the first to elucidate the nature of the orchid flower. He compared it with the structural and other morphological features of the flowers of certain allied monocotyledonous families and interpreted the labellum as a compound structure made up of the lateral stamens of the outer whorl and the median petal. Darwin, after studying the course of vascular traces in a considerable number of orchid flowers belonging to different tribes, incorporated the results in his monograph, "The Various Contrivances by which Orchids are Fertilised by Insects" (ed. 1899). In general, he confirmed Brown's observations, particularly with regard to the compound nature of the gynostemium and labellum.

Subsequent to this publication, very little has been

published on the vascular anatomy of orchid flowers. Even this meagre information is confined to the study of only teratological material. The present study is an attempt to understand the structural complexities of normal orchid flowers.

Material and Methods

Vascular anatomy of the flowers of the following genera have been studied; the number of species investigated in this study is indicated by a digit in parenthesis after each genus:

	Diandrae	
Cypripedilinae		*Paphiopedilum* (2)
		Cypripedium (1)
	Monandrae	
Ophrydinae		Habenaria § *Platanthera* (1)
		Habenaria § *Euhabenaria* (6)
		Habenaria § *Peristylus* (2)
		Satyrium (1)
Neottiinae		*Vanilla* (1)
		Zeuxine (1)
Coelogyninae		*Coelogyne* (2)
		Pholidota (1)
Liparidinae		*Oberonia* (2)
Phajinae		*Spathoglottis* (1)
Cyrtopodiinae		*Geodorum* (1)
		Eulophia (2)
Dendrobiinae		*Dendrobium* (3)
		Eria (1)
Bolbophyllinae		*Bulbophyllum* (1)
Cymbidiinae		*Cymbidium* (1)
Sarcanthinae		*Diplocentrum* (2)
		Luisia (1)
		Saccolabium (3)
		Vanda (1)
		Aerides (2)
		Rhynchostylis (1)

Material was fixed in formalin-acetic-alcohol, and serial microtome sections of the entire flower buds were prepared following the customary methods. Basic fuchsin or crystal violet, with a counter stain of light green, was employed for staining the vasculature and ground tissue respectively. This combination gave satisfactory contrast.

In addition to sectioning, entire flower buds of some species were cleared first in chloral hydrate and subsequently in lactic acid. This method was especially suitable for small flowers (like *Oberonia*, *Diplocentrum*, etc.) and those with delicate floral parts (like *Zeuxine*, *Habenaria*, etc.). But for larger flower buds (*Cymbidium*, *Eulophia*, *Dendrobium*, etc.), a certain amount of trimming of the perianth was essential.

After observing both serial sections and cleared material, wire-plasticine models were constructed, and the three dimensional drawings reproduced here have been sketched from such models. The *vascular diagrams* that accompany the text have been drawn as seen from above; however, the exact places of origin of certain traces have been slightly exaggerated and spread out in one plane in order to bring out the details.

Structure of the Flower

The orchid flower is bilaterally symmetrical. The ovary is inferior and bears at its upper extremity the other floral organs. There are two whorls in the perianth, each whorl consisting of three members. Often, all the members of the outer whorl are similar in appearance, though sometimes the median member (often designated as the "hood" or the "dorsal sepal") may be somewhat more conspicuous than the lateral members either in pattern or size. In the inner whorl of the perianth, the two lateral members are usually small and of the same shape as those of the outer perianth members, whereas the median

one is almost always very dissimilar both in size and shape, and is known as the "lip" or "labellum." Next are two whorls of stamens, which present definite variations of expression in the two great subdivisions of the family, Diandrae and Monandrae. In the former, the two lateral stamens belonging to the inner whorl are functional, and the median one of the outer whorl is represented by a conspicuous staminode, which assumes various shapes. No indications of other staminal members can be made out externally. In the Monandrae, on the contrary, the median stamen belonging to the outer whorl is the functional one and no indications of the other staminal members are to be seen externally. In both groups the next and innermost whorl consists of three stigmas; in the Diandrae, all three are usually functional, whereas, in the Monandrae, only the two lateral are functional, the median one being modified as the rostellum. Furthermore, it may be noted that the stamens and stigmas in the Diandrae are almost "free," whereas in the Monandrae they are united into a central pillar-like structure, which has come to be known by the names "column" or "gynostemium."

In the present text and the accompanying figures I am using the following terminology and symbols for the various parts of the orchid flower (reference to Fig. 1 may be made):

Outer whorl of perianth	Dorsal sepal	DS
	Lateral sepals	LS
Inner whorl of perianth	Median petal (labellum)	MP
	Lateral petals	LP
Outer whorl of stamens	Median stamen	A1
	Lateral stamens	A2 and A3
Inner whorl of stamens	Lateral stamens	a1 and a2
	Median stamen	a3
Whorl of stigmas	Median stigma	G1
	Lateral stigmas	G2 and G3

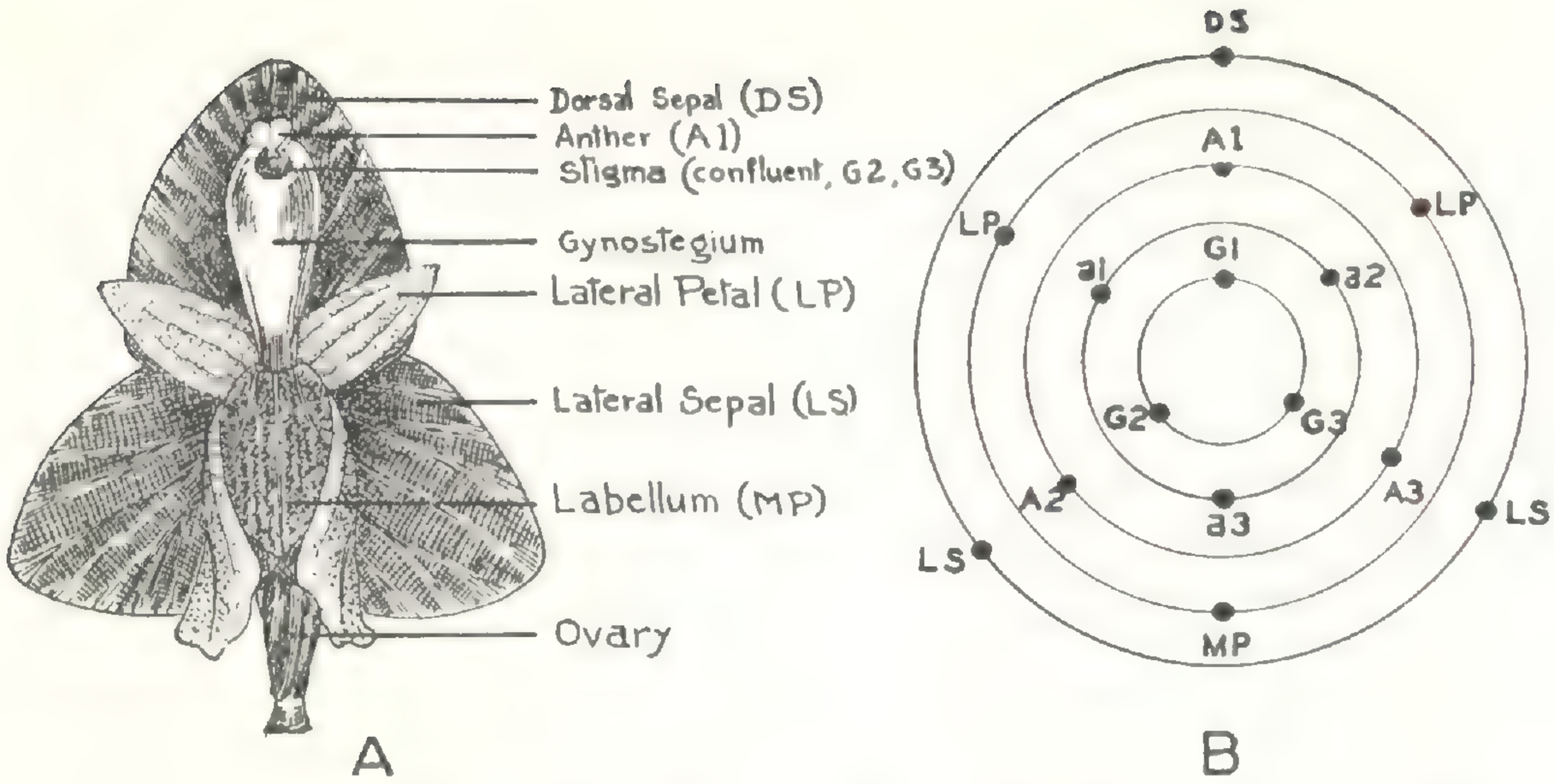

Fig. 1. A. A monandrous orchid flower showing its various parts.
B. Ground plan of the various vascular traces of a generalized orchid flower to indicate the symbols used in the text.

The orchid ovary, as will be seen presently, is traversed by six main vascular traces,* each lying under a perianth member; I am applying to these traces the abbreviations corresponding to the perianth members.

Main Vascular Traces of the Ovary

In the inflorescence axis of the orchids the vascular bundles are arranged in the same scattered pattern as in the vegetative axis of monocotyledons. The number of bundles that enter the floral axis and their method of breaking up into the six main traces of the ovary vary considerably in different genera. In *Paphiopedilum* and *Cypripedium* of the Diandrae (Fig. 2 A), six vascular bundles from the inflorescence axis deviate into the flower and constitute the corresponding main traces (DS, two LS, two LP and MP) of the ovary. The bract is supplied by a seventh independent bundle (Br) from the inflorescence axis.

*The term *trace* is used throughout this text to designate the vascular elements in the flower from the moment the vascular *bundles* of the inflorescence axis enter the ovary.

Among the monandrous orchids, usually three bundles from the inflorescence axis deviate into the floral axis and while doing so break up into the six main traces of the ovary. The exact method of their breaking up varies among the different genera. Further, the different levels at which they break up is also variable to some extent within the same species. In *Habenaria* (Fig. 2 B), two of the three bundles that deviate from the inflorescence

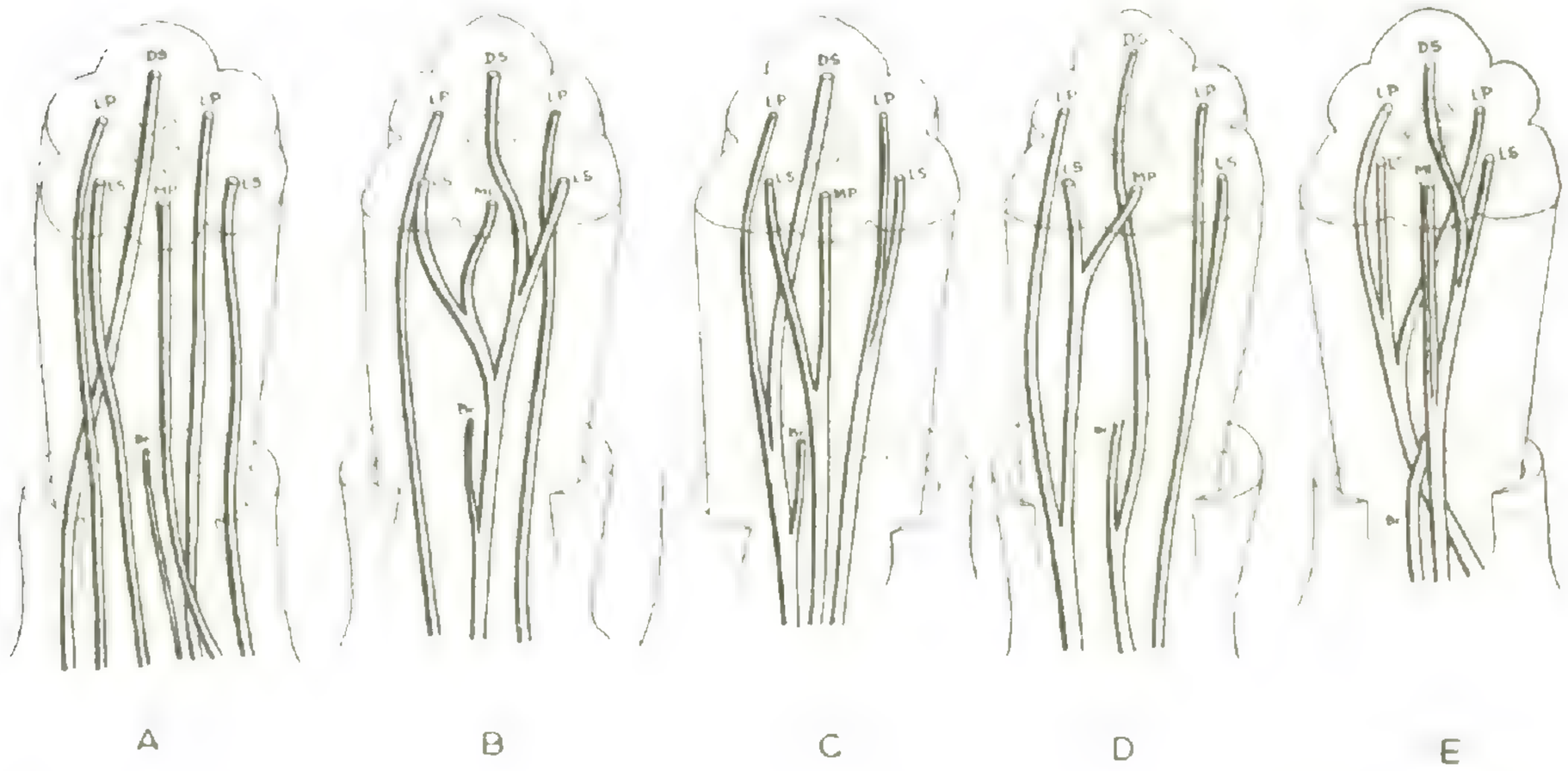

Fig. 2. A to E. Diagrams illustrating methods of the differentiation of the six main traces of the ovary from the vascular bundles of the inflorescence axis.

axis directly constitute those main traces of the ovary underlying the lateral petals (LP); the third bundle not only gives rise to the midrib trace of the bract (Br), but also, by further breaking up, constitutes the remaining four main traces of the ovary, underlying the dorsal sepal (DS), the two lateral sepals (LS) and the median petal (MP). In *Vanilla*, some species of *Dendrobium*, *Rhynchostylis* and a few others (Fig. 2 C), each of the three vascular bundles of the inflorescence axis that enters the flowers gives rise to two main traces of the ovary, the traces occupying positions under the adjacent perianth members (LP, DS; LP, LS; MP, LS); the median

trace of the bract (Br) is also given off by one of the three vascular bundles that deviates from the inflorescence axis. In *Bulbophyllum*, *Pholidota*, some other species of *Dendrobium* and a few others (Fig. 2 D), three vascular bundles from the inflorescence axis constitute the main traces of the ovary. One of the three breaks up into the median trace of the bract (Br) and the main trace of the ovary underlying the dorsal sepal (DS). The second, on bifurcation, forms the respective main traces underlying the lateral petal (LP) and lateral sepal (LS) of one side, whereas the third bundle gives rise to the remaining three main traces lying under the lateral petal (LP), the lateral sepal (LS) of the other side, and also to the median petal (MP). In *Cymbidium*, *Eulophia*, *Spathoglottis* and some members of the tribe Sarcanthinae (Fig. 2 E), though three vascular bundles from the inflorescence axis deviate into the floral axis, one of them constitutes only the midrib trace of the bract (Br). The second one gives rise to the main trace underlying the dorsal sepal (DS), one lateral sepal (LS) and median petal (MP). The third breaks up into the main traces underlying the lateral petals (LP) of both sides and the remaining lateral sepal. Thus in this instance only two bundles actually take part in the construction of the six main traces of the ovary.

The situation described above may be represented in the following tabular form (the vascular supply of the bract is omitted):

Tribe or genera	*Number of bundles deviating from the inflorescence axis into the floral axis*	*Method of further breaking up of the bundles of the inflorescence axis*
Cypripedilinae (Fig. 2 A)	6	No further differentiation; but directly constitute the six main traces of the ovary,—DS, LS, LS, LP, LP, MP.

Ophrydinae (Fig. 2B)	3	1 (LP)+4 (DS, LS, MP, LS)+1 (LP)
Vanilla, *Dendrobium*, *Rhynchostylis*, *Aerides*, etc. (Fig. 2C)	3	2 (LP, DS)+2 (LP, LS) +2 (MP, LS)
Oberonia, *Bulbophyllum*, *Coelogyne*, *Pholidota*, etc. (Fig. 2 D)	3	3 (LP, LS, MP)+1 (DS) +2 (LP, LS)
Cymbidium, *Eulophia*, *Spathoglottis*, some members of Sarcanthinae, etc. (Fig. 2 E)	2	3 (LP, LP, LS)+3 (MP, LS, DS)

From the preceding account it will be clear that, from the standpoint of the origin of traces, there is no basis for distinguishing the main traces that belong to the outer whorl from those that belong to the inner whorl of the perianth. Actually, the bundles of the inflorescence axis that enter the flower split up in a variety of methods and constitute the six main traces of the ovary. Neither does there seem to be anything in the position of the traces themselves to distinguish the two whorls, because in transverse sections the six main bundles are arranged more or less on one and the same circumference (Fig. 3 A). There is also no difference between the traces of the two whorls with respect to size or degree of expression. Even those main traces that adjoin the placentae (LP, Fig. 3 B), which in other groups usually show an exaggerated development either in size or proliferation, in this case look exactly similar to the traces lying on alternating radii (DS, Fig. 3B).

In some orchids with large-sized labellum (like *Cymbidium*, *Eulophia*, *Spathoglottis*, etc.) the main trace underlying this modified petal (MP) shows a double nature (Fig. 2 E). It may be argued by some that this feature may be due to the size-relation of the organ which it is supplying. The weight of this argument becomes

invalidated when we consider the fact that the corresponding trace in orchids like *Cypripedium* and *Paphiopedilum*, which possess labella of much larger size and display than those of *Cymbidium* or *Eulophia*, is always single.

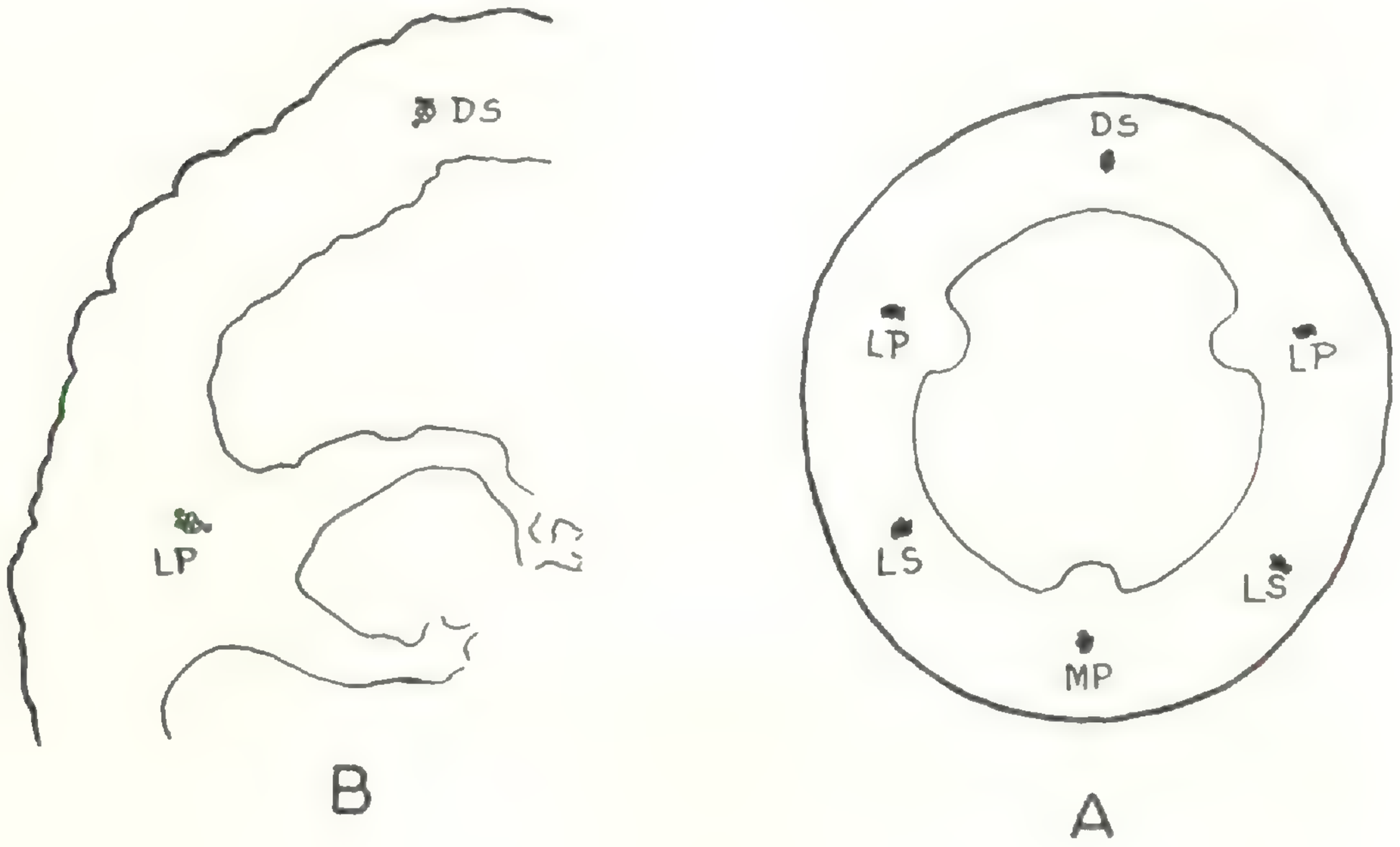

Fig. 3. A. Transverse section of an ovary showing the disposition of the six main vascular traces running in its wall. B. A portion of a transverse section of an ovary enlarged; traces DS and one of its adjacent LP are shown.

Another point which may be noted here is that the traces running along the placentae and underlying the inner whorl of perianth members do not show any signs of breaking up and supplying any part of the placentae. Hence the ovules are totally devoid of any kind of vascular supply.

Types of Vasculature in the Flower

The six main traces of the ovary begin to break up further into the various traces of the floral whorls and organs just below the level of insertion of the perianth. Though the general scheme of splitting is essentially the same in all the orchids investigated, three distinct types

may be recognized on the basis of the origin and nature of the vascular supply to the staminal and stigmatic whorls, rather than on the method of vascular supply to the perianth.

Type I. (Seen in the members of Cypripedilinae; Fig. 4 A, B and C). The traces to the median and lateral stigmas (G1, G2, G3) are the first to be separated. As can be expected, they arise from the main traces, DS and the two LS, underlying the median and lateral sepals respectively. At a slightly higher level, the same main traces trifurcate, to constitute the median and marginal traces of the respective perianth member. Further, the marginal traces of these sepal members supply the marginal traces to the petals also (Fig. 4 A). The main trace, DS, gives rise to another small trace (A1) at a slightly higher level; this trace runs vertically into the staminode.

The main traces occupying positions under the lateral perianth lobes of the inner whorl, after giving out the traces to the functional stamens (a1 and a2), merely pass into the respective petal as its median trace. The marginal traces of these, as has been stated, are derived from branches of marginal traces of the sepal members. The main trace, MP, does not split up but continues into the labellum as its median trace.

The following points may be especially noted in this connection:

1. Masters (1887) observed in some species of *Cypripedium* that the trace underlying the labellum also trifurcated to form the median and marginal traces of that petal. However, the flowers here examined do not show this feature. The marginals of the labellum are always given out by the marginal veins from its adjacent sepal members.

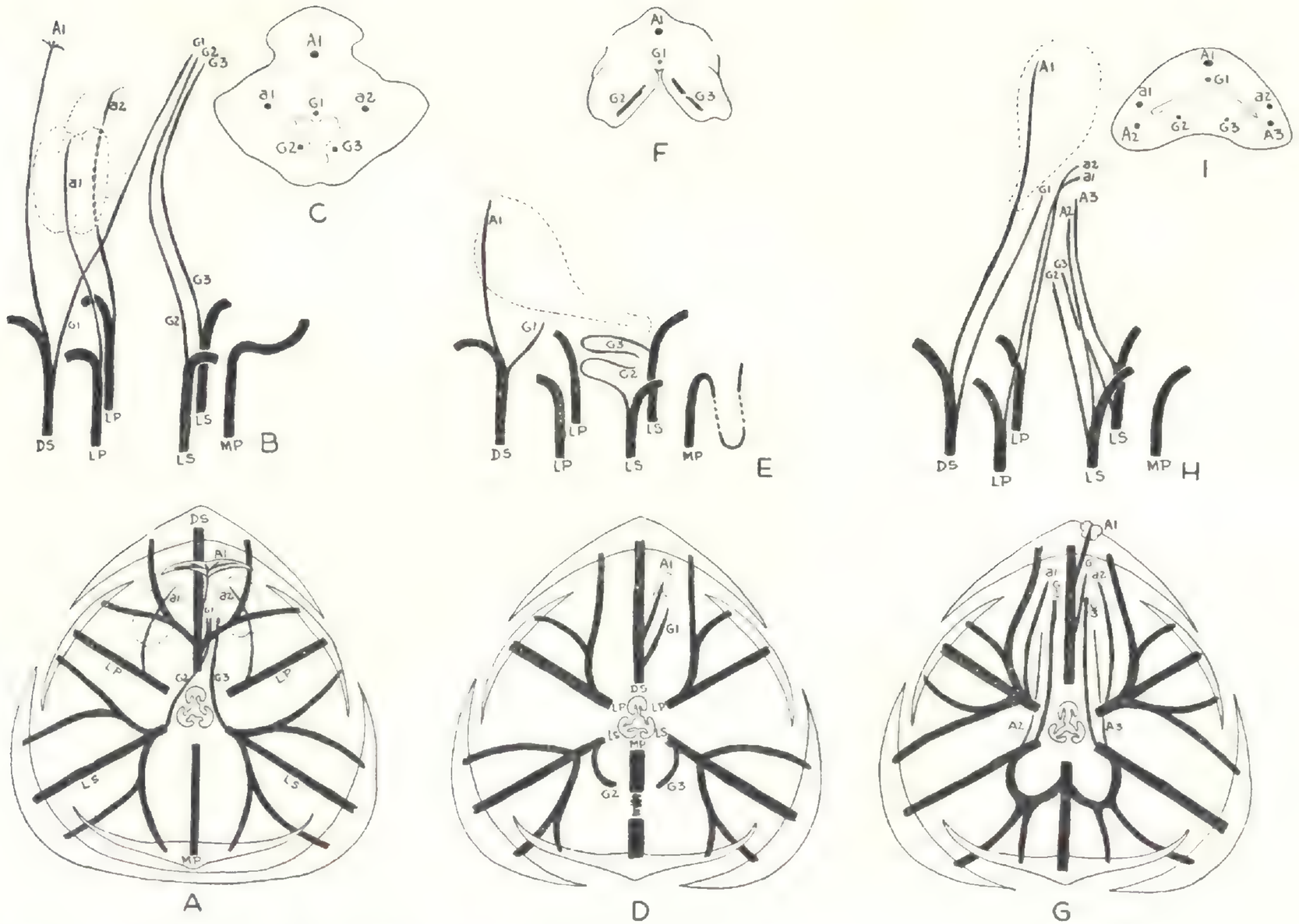

Fig. 4. A, B and C. *Paphiopedilum*. D, E and F. *Habenaria*. G, H and I. A monandrous orchid. A, D and G are vascular diagrams; B, E and H are drawings from wire-plasticine models; C, F and I are transverse sections at the region homologous with the gynostemium.

2. The vascular traces supplying the staminode, functional stamens and stigmas, all run only for a very short distance in a common tissue; hence a definite structure like the gynostemium is almost absent or highly reduced in these plants. However reduced this structure may be, the following six vascular traces may always be recognized in a transverse section (Fig. 2 C):

a. A 1 occupying a dorsal median position,
b. a 1 and a 2 occupying a lateral position, and
c. G 1, G 2 and G 3, all three together occupying a place just below A 1.

3. Link (1849) thought that the fertile lateral anthers of Cypripedilinae originated by the division of the median stamen, the staminode being looked upon as an enormously developed connective. Masters' observations on teratological material have already cast a doubt on the tenability of this view. The present studies also suggest that Link's interpretation is erroneous.

Type II. (Seen in the members of Ophrydinae; Fig. 4, D, E and F). The main trace, DS, gives rise to the traces that supply the median stigma (G 1), the median stamen, A 1, and the median trace of the corresponding sepal. The marginal traces for this sepal are supplied by the main traces underlying the lateral petals (LP). The main trace (MP) does not give rise to any other trace excepting the median one of the labellum and its spur, which is merely a downward pouch-like extension of the labellum; the marginal traces are supplied by those of the adjacent perianth lobes of the outer whorl (LS). The main traces underlying the lateral sepals, in addition to forming the median and marginal traces of these lobes, give rise to the traces, G 2 and G 3, which supply the lateral stigmas.

It may also be noted that the marginal traces of the

lateral petals are altogether absent in *Habenaria* § *Platanthera;* the marginal traces towards the dorsal sepal alone are present in *Habenaria* § *Peristylus;* and in some species of *Euhabenaria*, their presence is occasional and often they are very poorly developed.

A transverse section passing through the gynostemium at the level of the stigmas (Fig. 4 F) shows the following four vascular traces:

a. A 1, representing the supply to the functional stamen (median) of the outer whorl, and
b. G 1, G 2 and G 3, supplying the median and lateral stigmas respectively.

Generally the members of Ophrydinae possess a spur. Morphologically this structure is nothing but a downward outgrowth of the labellum in the form of a long tube or sac. *Satyrium nepalense* has a double spur; it is also dorsal in relation to the inflorescence and flower, as there is no resupination. Where the spur is single, the median trace of the labellum runs throughout its entire length and finally continues upwards into the labellum (Fig. 5 A). The marginal traces of the labellum (that are derived from the adjacent sepal traces), however, do not enter the spur but curve up into the expanded portion of the labellum (Fig. 5 A). On the other hand, where the spur is double, the median trace of the labellum does not enter the spur but runs straight into the median petal as its median trace; the marginal traces (that are given off by the adjacent sepal traces) run throughout the length of the spur on that side and then continue into the median petal as its marginal traces (Fig. 5 B).

Type III. (Seen in the majority of monandrous orchids. Fig. 4 G, H and I). The first traces to be separated off at the level of insertion of the perianth are those to the three stigmas (G 1, G 2 and G 3), given off by the

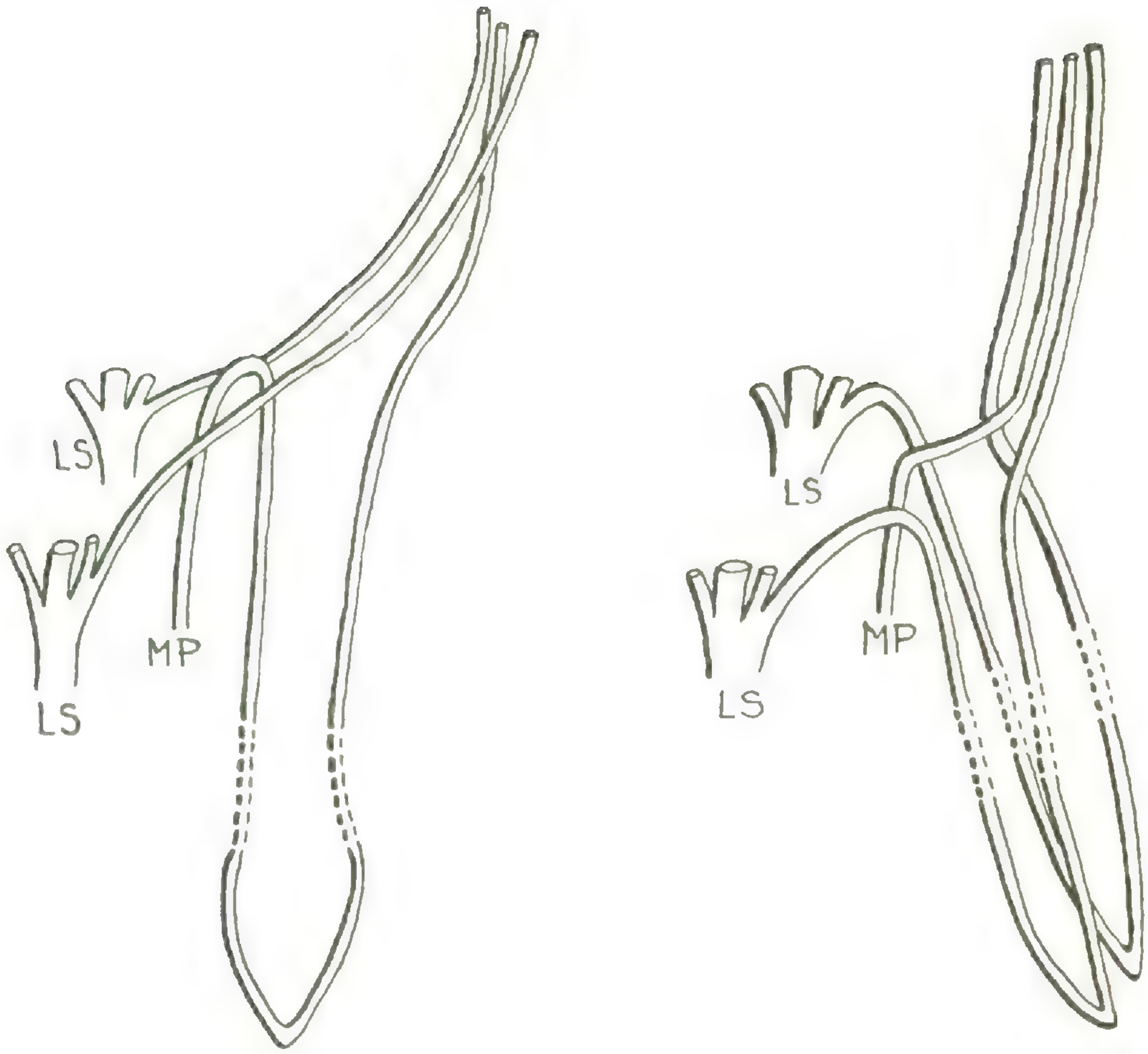

Fig. 5. Drawings from wire-plasticine models to illustrate the nature of the vascular supply to the labellum and spur.
A. When the spur is single; B. When the spur is double.

main traces underlying the sepals. Then, in some genera, each of the main traces underlying the lateral petals (LP) gives off a trace (a1 and a2) into the gynostemium, these representing the lateral stamens of the inner whorl. In some other genera, the main traces of the lateral sepals (LS) each give out a trace (A2 and A3) into the gynostemium; these represent the traces belonging to the lateral stamens of the outer whorl. The commoner condition is the presence of the traces representing the lateral stamens of the inner whorl. In some genera (*Dendrobium*,

Cymbidium, etc.), both sets of lateral stamens (A 2, A 3 and a1, a2) may be present. It must be stated here that the expression of the staminal traces is highly variable in different genera and is often associated with highly complicated types of adnation. (This phenomenon is treated in detail in a later part of this text under "Comparative Resumé of the Vascular Supply of the Stamens." See page 77). After supplying the vasculature to the stamens and stigmas, the residue of the main traces (excepting the one under the dorsal sepal) breaks up further to constitute the vascular traces of the perianth lobes. (Variations of the vasculature of the perianth members of this type are explained in a later part of this text under "Comparative Resumé of the Vascular Supply of the Perianth." See page 76).

The following points may be noted in connection with this type:

1. The gynostemium (Fig. 4 I) contains the following traces:

   a. A 1 supplying the median stamen of the outer whorl, which is the functional one,

   b. G 1, G 2 and G 3, reaching the rostellum and the confluent lateral functional stigmas, and

   c. either a1 and a2 representing the traces of the lateral stamens of the inner whorl, or A 2 and A 3 representing the lateral stamens of the outer whorl, or both.

2. The traces of the staminal and stigmatic whorls are all embedded in a well-developed pillar-like structure (a gynostemium).

Types I and II are consistent; no marked variations were seen. But Type III is subjected to a high degree of plasticity. This is closely associated with increasing cohesion, adnation and other phenomena which are described in the following paragraphs.

Comparative Résumé of the Vascular Supply of the Perianth

In minute flowers like those of *Oberonia* and in the flowers of the semi-saprophyte, *Zeuxine*, the vasculature is very poorly developed. As a result, the system is not attended by any secondary modifications (Fig. 6, B). In flowers like those of *Vanilla*, *Coelogyne*, etc., the marginal traces of the adjacent perianth members lie close together (Fig. 6 C). In *Dendrobium*, *Bulbophyllum*,

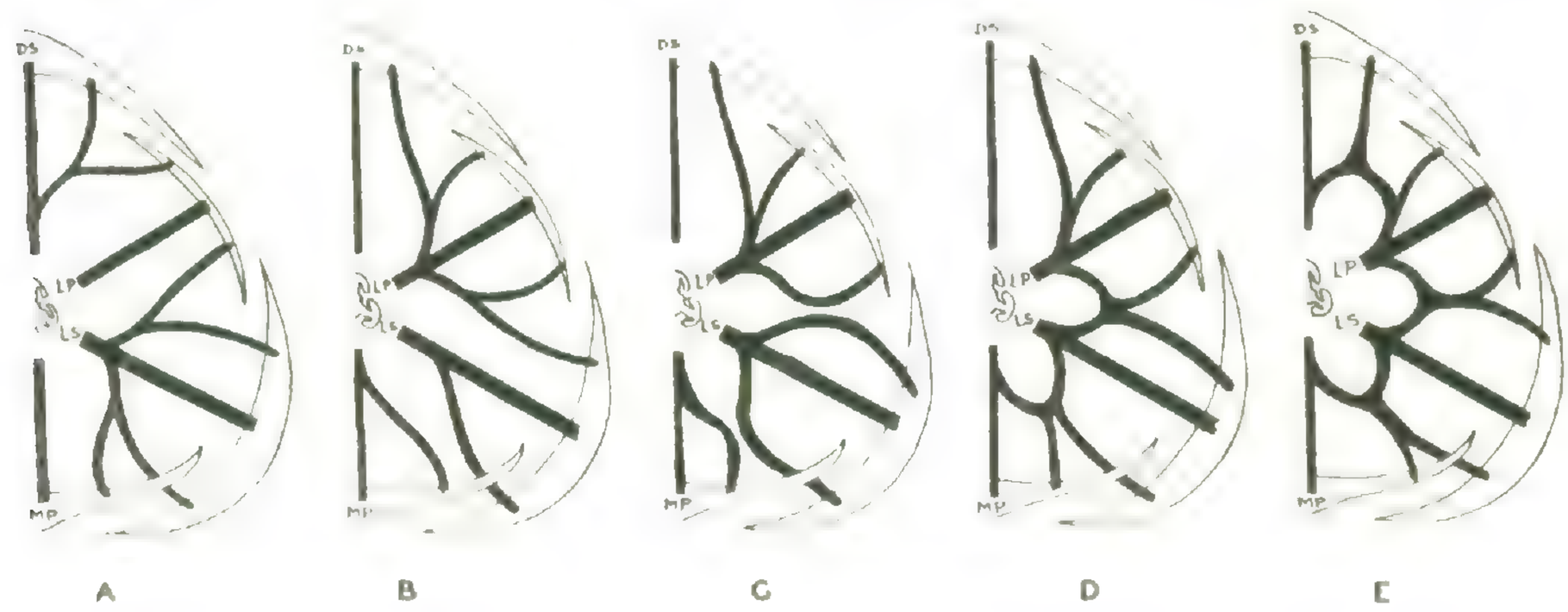

Fig. 6. A to E. Series of diagrams to illustrate the increasing complexity of the vascular supply of the perianth members. Only one-half of the flowers is shown; traces to the stamens and stigmas are not shown for the sake of avoiding confusion.

Pholidota, *Spathoglottis*, etc., the marginal traces fuse to form an "arch" and from this point again separate out (Fig. 6 D). In *Cymbidium* and many members of the tribe Sarcanthinae, the marginal traces after forming an "arch" proceed in a fused condition for a considerable distance and then separate (Fig. 6 E). Often some of the marginal traces even enter the respective perianth member in the fused condition (see the marginal trace of the dorsal sepal in Fig. 6 E).

It may also be noted that the main trace, DS, does not in general give rise to any of the marginal traces of the dorsal sepal. But when it does split up into the marginal traces, as in *Cymbidium* and some members of the Sar-

canthinae, it invariably anastomoses with those of the adjacent lateral petal.

Another feature to be noted is the origin of the marginal traces of the adjacent perianth lobes. Usually the marginal traces of the outer perianth members are derived from the traces underlying the perianth members of the inner whorl or *vice versa*.

Comparative Résumé of the Vascular Supply of the Stamens

A lack of proper understanding of the vasculature of the staminal whorls, in the past, seems to have been the cause of the confusion prevailing today with regard to the exact composition of the androecium of orchids. In this connection two points need clarification,—(A) the number of staminal traces that are given off and their identity, and (B) the method by which a simple origin becomes increasingly complicated through the intervention of adnation. It is difficult to separate the two aspects which are so closely associated in orchids; but for the sake of convenience of description, I propose to treat the two points under the headings (A) and (B), as mentioned above.

A. It has already been pointed out that in the Cypripedilinae the two lateral stamens of the inner whorl (a1 and a2) are functional and that the median stamen of the outer whorl (A 1) is externally represented by a staminode, which also receives a vascular trace. Furthermore, it has also been mentioned that in the monandrous orchids it is the median stamen of the outer whorl (A 1) that is functional and that quite often the lateral stamens of the inner whorl (a1 and a2) are represented only by vascular traces. The presence or absence of the traces cannot be made out by any external morphological distinctions.

It may be recalled that in some species the traces for the lateral stamens of the outer whorl (A 2 and A 3) may also be represented and that in many instances all of the four lateral stamens may be represented by their corresponding vascular traces in varying degrees of expression : that is, the traces themselves may be so rudimentary that they do not run even to the base of the gynostemium, or they run up only a short distance into the structure, or they may even reach the distal end of it. The degree of expression may affect one, two, three or all of the four lateral staminal traces. The latter condition may be frequently seen in *Zeuxine*, *Oberonia*, *Eria*, etc.

Clear-cut examples where either the lateral stamens of the inner whorl alone or only those of the outer whorl manifest themselves are seen in *Eulophia*. In *E. nuda* (Fig. 7 A and B) the main traces (LS) underlying the lateral perianth members of the outer whorl, after giving off the traces G 2 and G 3 to the respective stigmas, separate out correspondingly the traces A 2 and A 3. That

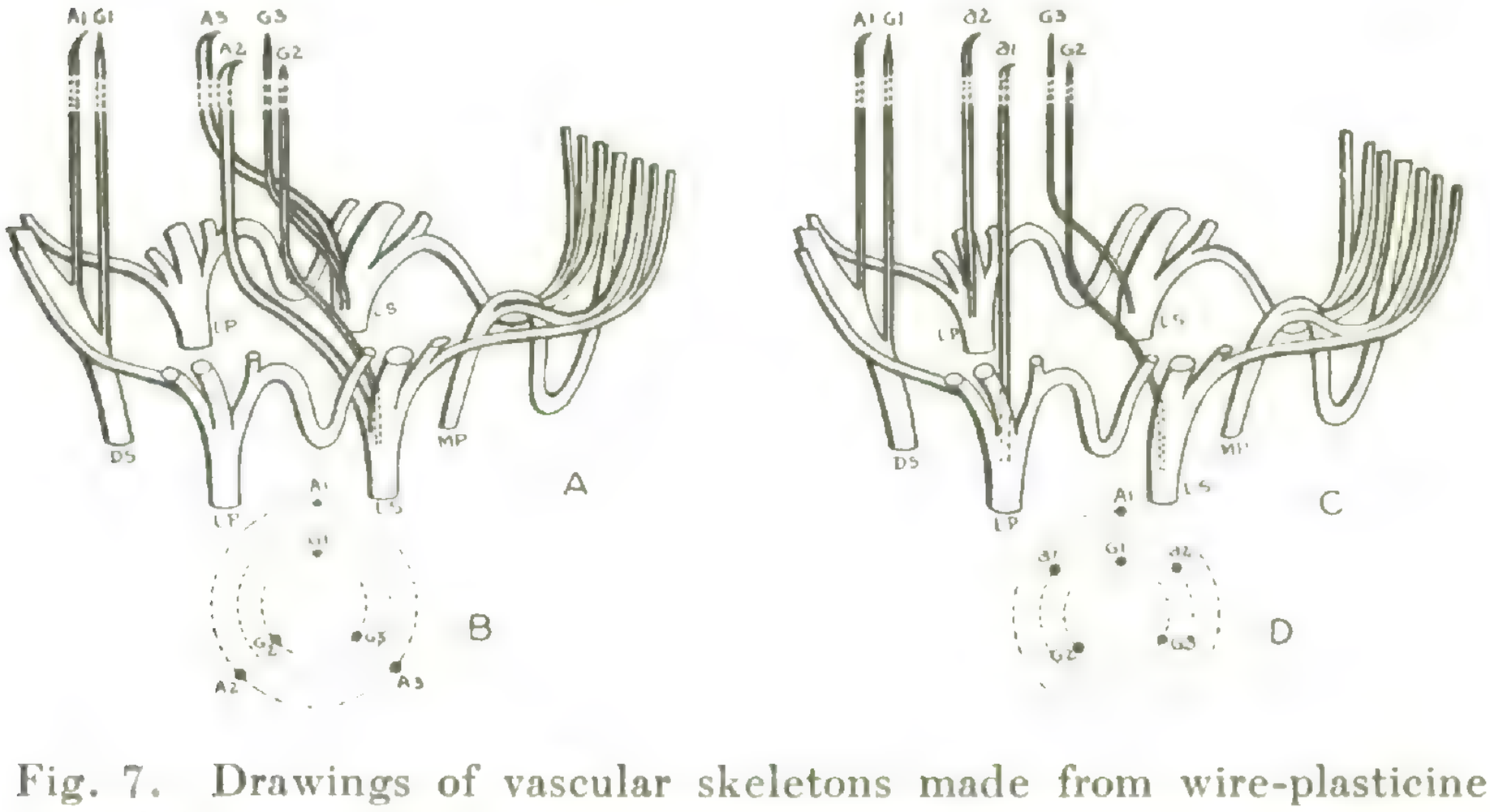

Fig. 7. Drawings of vascular skeletons made from wire-plasticine models illustrating the splitting up of the six main vascular traces of the ovary into the vascular supply of various whorls. A and B. *Eulophia nuda;* C and D. *Eulophia epidendraea*. In B and D the staminal and stigmatic traces are shown as rearranged according to their status; vascular traces of the perianth members are omitted in these.

these traces represent only the lateral stamens of the outer whorl and that these cannot be considered to be otherwise is proved by the fact that they originate after the stigmatic traces have been separated off and before the trifurcation which results in the formation of the median and marginal traces of the respective perianth member. In *E. epidendraea* (Fig. 7 C and D), the main traces, LP, underlying the lateral petals, before splitting up to form the supply to the corresponding perianth members, give out the traces a1 and a2 which obviously represent the traces for the lateral stamens of the inner whorl. That these traces cannot be interpreted otherwise is borne out by the point of their separation from the main trace, LP.

B. In other orchids, the degree of expression of the traces for the stamens of the two whorls is complicated by the associated phenomenon of adnation. The series of diagrammatic illustrations in Fig. 8 is intended to convey the increasing complexity in the origin of the staminal traces. In these figures the behavior of one pair of the main traces (LP and LS) underlying the lateral perianth members of one side of the flower is shown. A illustrates the simplest condition where there is no fusion; the staminal traces a2 (belonging to the inner whorl) and A3 (belonging to the outer whorl) are quite distinct both in origin and further course. In B, the two traces are still distinct; but their separation from the respective main traces is postponed until after the trifurcation of the main traces themselves; thus the position of the origin of the staminal traces is carried up to a higher level in relation to the floral axis. In C, the position of origin of the two staminal traces is carried up still higher; they originate at a point nearer to the anastomosing point of the marginal traces. Furthermore, the two staminal

traces come to lie closer soon after separation and seem to fuse with one another and then proceed upwards in the gynostemium. D illustrates the climax of this tendency. The origin itself of both the staminal members is carried higher to a point where the adjacent marginal traces fuse and thus their distinctness becomes totally obliterated. Further, the marginal traces of the respective perianth

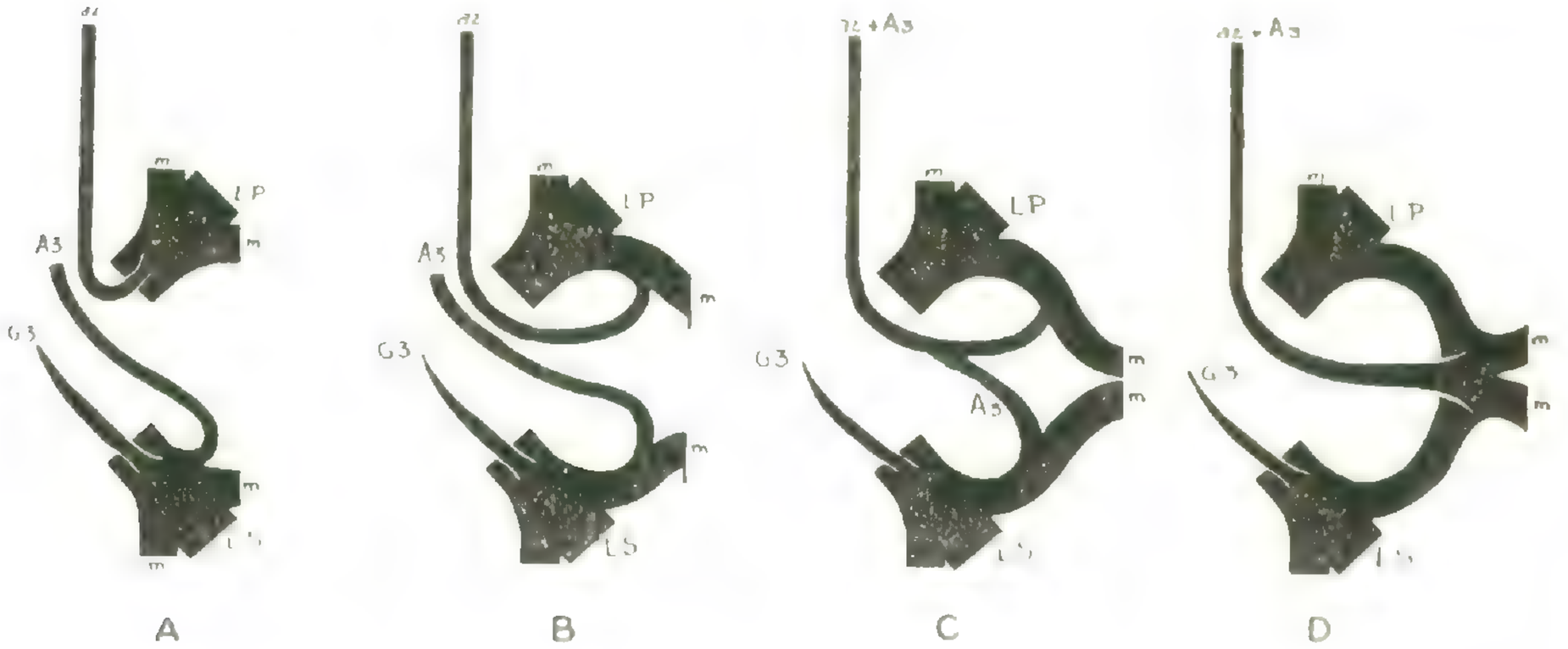

Fig. 8. A to D. Diagrams to illustrate the evolution of "compound" staminal traces, a2+A3.

member are also separated from the same point. Thus the nature of the staminal trace in this instance becomes "compound" by the adnation of a lateral stamen of the inner whorl with that of a lateral stamen of the outer whorl, and as a consequence such traces have been here interpreted and represented as a1 + A 2 or a2 + A 3, as the case may be.

The degree of expression of adnation is often seen to vary in one and the same species. *Geodorum densiflorum* may be taken as a good example to exhibit this phenomenon; furthermore, this orchid also throws some light on the fundamental nature of the androecium of the family. Normally in this species, in addition to A 1, the lateral stamens of the two whorls are also represented by "compound" traces, a1+A 2 and a2+A 3 (Fig. 9 A and B).

As has been stated more than once, the vascular pattern is not always strictly fixed, but is somewhat plastic in this species. In all of the three instances of deviations to be described below, the origin and nature of the trace A1 is very consistent, as in the other monandrous orchids. It is the nature of the other vascular traces of the staminal whorls that present interesting variations. In the first deviation (Fig. 9 C and D) the staminal vascular traces arise from the point of trifurcation of the main traces, LS. Thus the traces A2 and A3 complete the outer whorl of stamens. In the second deviation (Fig. 9 E and F), the main trace under one of the lateral sepals give rise to the trace A2 (representing a lateral stamen of the outer whorl), whereas on the opposite side the main trace lying under the lateral petal gives the trace a2 (representing a lateral stamen of the inner whorl). In the third deviation (Fig. 9 G and H, left), there arises a compound staminal trace, a1+A2, whereas on the opposite side the main trace under the lateral sepal gives rise to A3, representing a lateral stamen of the outer whorl). In addition to these two, the main trace, MP (lying under the labellum), also sends out a slender offshoot, a3, into the gynostemium; this trace is to be interpreted only as representing the median stamen of the inner whorl. Thus, these deviations, when taken together, reveal the presence of all of the six stamens belonging to the two whorls. This also makes it possible to visualize the fact that all of the six stamens were once functional in the ancestral orchid flower.

In passing, it may also be noted by a study of these illustrations (Fig. 9) that the plasticity of vasculature is not confined to the staminal whorls alone but is extended to the labellum also, whereby the latter is supplied by supernumerary marginal traces in certain instances.

Before proceeding to the general discussion, it is im-

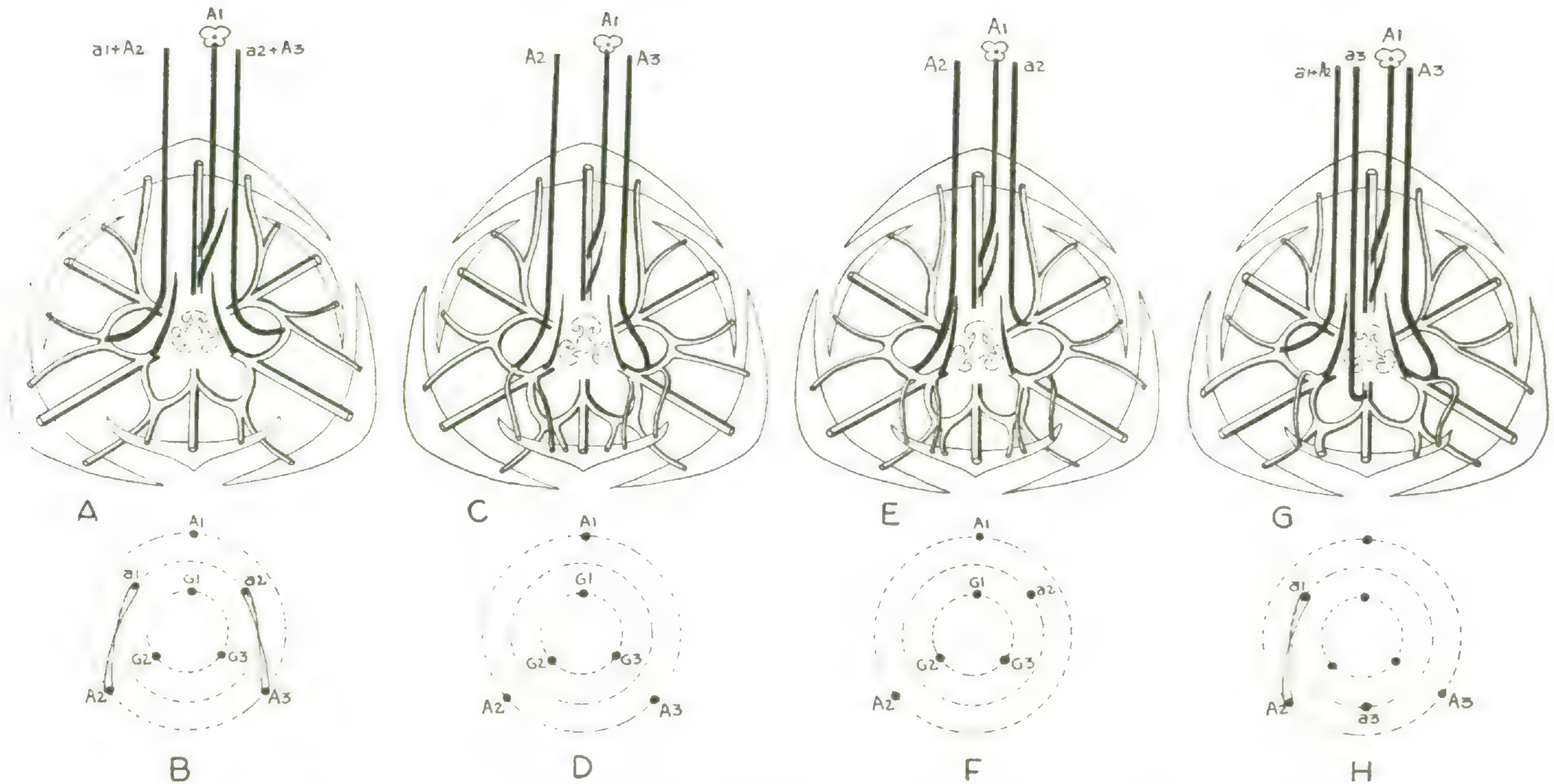

Fig. 9. A, C, E and G. Vascular diagrams of the normal and three deviation patterns respectively of *Geodorum densiflorum*. Traces belonging to the stamens and stigmas are shown in solid black. B, D, F and H. Staminal and stigmatic traces of A, C, E and G respectively, arranged according to their status.

portant to have an idea of the changes that are brought about in the vascular pattern of the flower during the development of the flower itself. This type of study was confined only to *Dendrobium* and *Cymbidium*, but I feel that the results obtained may in general be applicable to other orchids also. Here again, particular attention may be laid upon the development of "compound" staminal traces.

In the young condition (when the microsporangium is just differentiated) the marginal traces of the adjacent lateral petal and sepal show the following features (Fig. 10 A): The staminal traces a1, a2, A 2 and A 3 are all distinct from one another, although their place of origin is shifted higher up to the point of concrescence of the adjacent marginal traces; but actual concrescence is not yet affected. During subsequent development, concrescence and adnation proceed to such a degree that the distinct origin of the staminal traces becomes totally obliterated so that they are seen only as "compound"

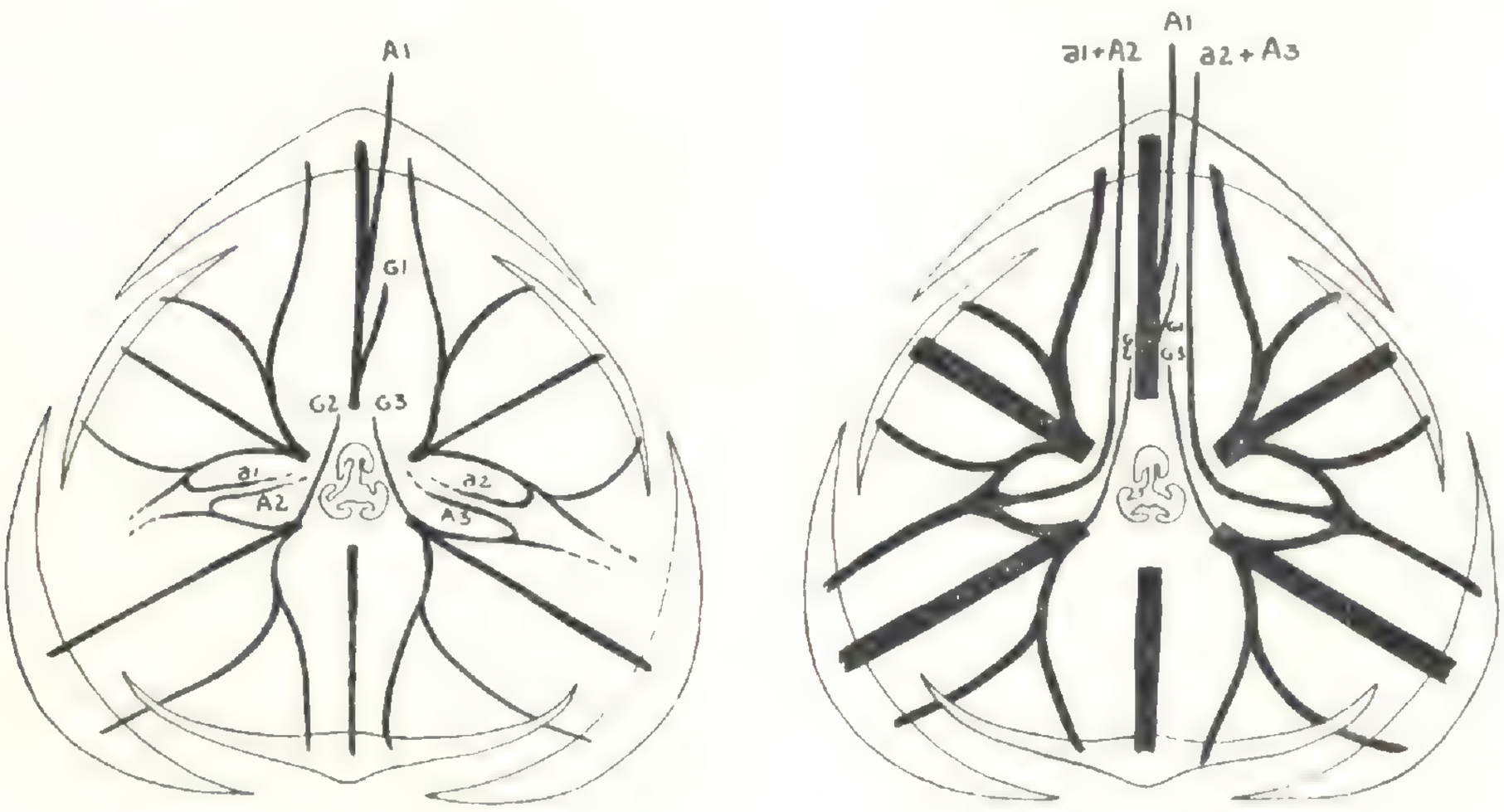

Fig. 10. Vascular diagrams of *Dendrobium* showing the juvenile condition in A and the adult condition in B.

traces (Fig. 10 B); thus the traces for adjacent lateral stamens of the one side are represented by the compound trace, a1+A2, and on the other side by the similar trace, a2+A3.

General Discussion

Ovary. In recent years the nature of superior and inferior ovaries has raised a good deal of controversy. The evidence at hand points out that the inferior ovary in at least the majority of instances is a product of adnation of floral whorls, though there seems to be some evidence as to its receptacular nature in a few genera or groups of plants. The orchid ovary, as has been said before, is traversed by six main vascular traces that run throughout the length of the ovary proper without any kind of splitting, and the further division begins only at about the insertion level of the perianth and other floral organs. This condition may be looked upon as a result of adnation in its extreme degree of expression. The irregularity seen in the method of origin of the six main traces of the ovary in different genera of orchids may also be correlated in some way with the high degree of adnation.

Perianth. The whorls of perianth members externally suggest considerable distinctness. In general, those of the outer whorl are uniform in appearance, whereas those of the inner whorl are variable. Particularly does the labellum (median petal) assume a series of varied patterns in size, shape and color. Whatever may be the outward manifestation, internally each of them (sepals as well as petals) receives a median and two marginal traces. Quite often the marginal traces of one whorl of the perianth members are derived from the traces belonging to the perianth members of the other whorl. Anatomically, all of the perianth members are thus of the

same category. The 3-trace supply is more a characteristic feature of sepals than of stamens. From these considerations, the perianth of orchids seems to be more sepaline in character.

Ontogeny of the flower, in some cases, has been sought to elucidate the nature of the petals—whether they are akin to sepals or stamens. Thus Goebel (1933) correlates the belated appearance of petals during the ontogeny of the flower with their nearness to stamens. In the orchids the ontogenetic order of appearance of floral whorls is centripetal (Swamy, 1946; also unpublished data). And even when Goebel's correlation is applied to the condition in orchids, it is seen that the petals are not allied to stamens but to sepals.

Labellum. This structure of the orchid flower has been the target for much dispute. Brown (1831) put forward the doctrine that the labellum is a compound structure resulting from the fusion of some of the staminal members with the lip. However, he did not offer sufficient evidence for his opinion and also was not certain as to which of the stamens enter into fusion. He further suggested that such a fusion was especially responsible for the extra-conspicuousness of the labellum with ridges and crests in some orchids. Lindley (1840) followed this view. Darwin (1899), after studying the course of vascular traces in some orchids, came to the same conclusion: "The Orchid flower consists of five simple parts, namely, three sepals and two petals; and of two compound parts, namely, the column and labellum. The column is formed of three pistils and generally of four stamens, all confluent. The labellum is formed of one petal with two petaloid stamens of the outer whorl, likewise completely confluent." As Darwin thus elaborated and confirmed Brown's ideas, the authorship of the compound theory

of the labellum is attributed both to Brown and Darwin (see Fig. 11, which gives a diagrammatized interpretation of a monandrous orchid flower according to Darwin's conception).

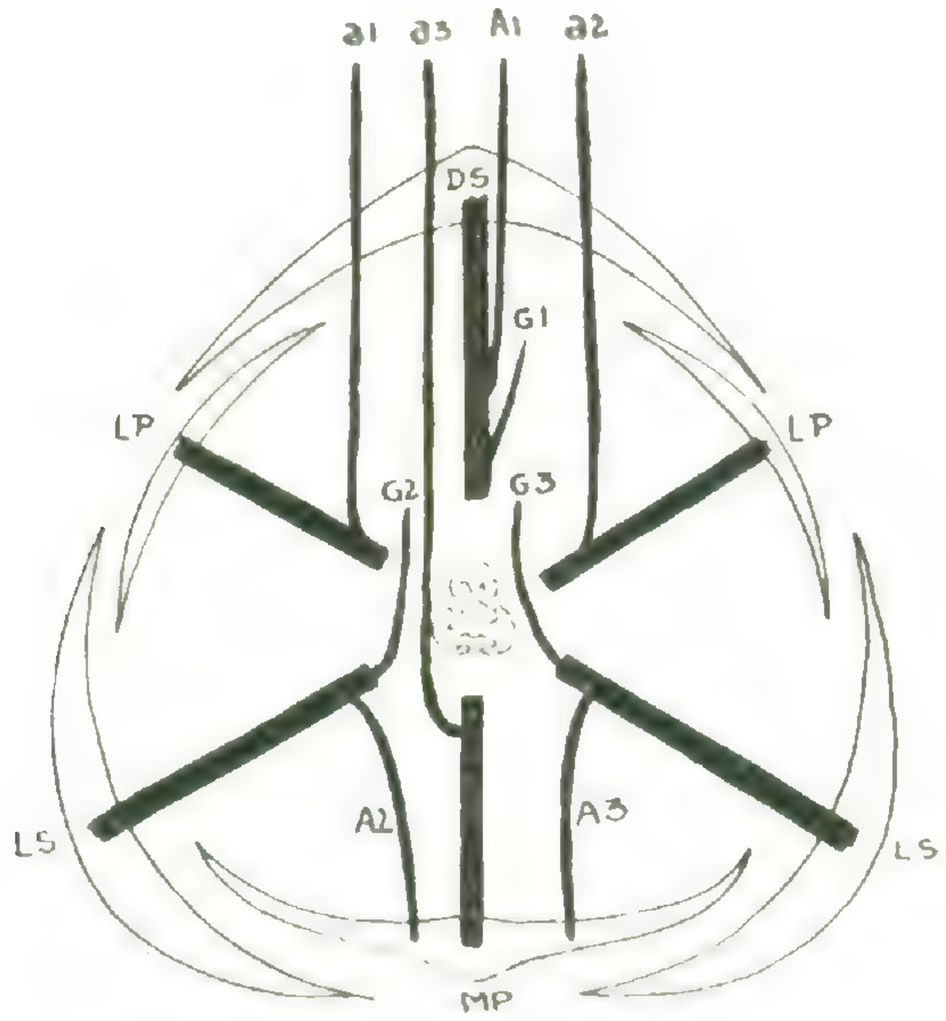

Fig. 11. Vascular diagram of a monandrous orchid flower reconstructed according to the description of Darwin.

The Brownian and Darwinian conception of the orchid labellum held sway for a long time, influencing subsequent studies to a great extent. Many reports on teratological orchid flowers were interpreted in the light of this hypothesis and were brought forward as evidences in favor of it. Even as recently as 1937, Saunders, while attempting to advocate her theory of "carpel polymorphism," fully accepted the old hypothesis, ignoring the opposition brought forward in refutation of the Brownian and Darwinian views of the orchid labellum.

Crüger's views (1865) which are contrary to the compound concept of the labellum seem to have been ignored until 1916, when Worsdell brought out his two volumes of "Principles of Plant Teratology." In this publication, Worsdell has accumulated all of the points adduced in favor of the compound nature of the labellum and has

given his own alternative interpretations of the very examples which were previously interpreted as evidencing the old hypothesis. He also summarizes other instances "which decidedly seem to tend towards disapproving the accepted theory and to support that advanced by Crüger." In addition to these, he presents some of his own original observations on some abnormal flowers of *Cypripedium*. All of these combine to support the opinion that there is not even a single instance to support the view of the compound nature of the labellum.

As can be seen, until now the Brownian and Darwinian concept of the orchid labellum has largely been checked only with teratological flowers. Excepting the study of Masters (1887), which deals in part with the vascular anatomy of normal flowers, I am not aware of other subsequent contributions dealing with the anatomical studies of normal orchid flowers.

The present anatomical study of 40 species of orchid flowers belonging to 24 genera also does not show any evidence in support of the compound theory of the labellum. The traces representing the lateral stamens of the outer whorl, whenever present, are distinctly identifiable in the gynostemium. Their independent origin and course is especially clear in forms like *Eulophia*, where no kind of secondary fusion nor complication accompanies their expression. Even in those instances where adnation results in a compound staminal supply as a1 + A2 and a2+A3, the traces without an exception pass into the gynostemium but not into the labellum. Furthermore, the labellum is almost always provided with separate marginal traces, given out by the veins belonging to the adjacent perianth members. As has already been stated in an earlier part of this text, the labellum receives typically a median and two marginal traces and hence is in no way different anatomically from other perianth members.

From a consideration of these facts, the only reasonable conclusion that can be arrived at is that the labellum is not a compound structure as was supposed by Brown and Darwin. It may also be noted here that those instances in which the marginal traces of the labellum were not in evidence or exhibited abnormal behavior when present offered difficulties of interpretation to Darwin himself. For he writes: "This anomaly is so far of importance, as it throws some doubt on the view that the labellum is always an organ compounded of one petal and two petaloid stamens."

Spur. This structure, as has been explained already, is a basal outgrowth from the labellum in the form of a pouch, sac or narrow tube. Where the spur is single, the median trace of the labellum continues into it and then recurves upwards in conformity with the curvature of the spur to constitute the median trace of the same petal. When the spur is double, the median trace of the labellum does not enter the spur but each marginal trace enters into the spur of the corresponding side. In passing, it may be mentioned that Darwin thought the traces that traverse the double spurs were staminal (A2 and A3). That Darwin's views are untenable has already been made clear.

Gynostemium. This is a structure peculiar to the orchid flower. Its exact nature has, until now, been little understood. Chiefly the works of Oliver (1895), Rendle (1930) and Willis (1936) have propagated the idea that this structure is an extension of the floral axis and that on this account it is to be looked upon as being axial. It may be recalled that such a distinct structure is not clearly evidenced in *Cypripedium*, *Habenaria*, etc. In the former, it is incipient if it is present at all; serial

microtome sections alone can reveal its incipient condition anatomically. In all of the other orchid flowers studied at this time the structure is well-developed; and in all such species, it is an appendicular structure containing the vascular traces supplying the staminal and stigmatic whorls. The morphological apex of the flower, therefore, does not extend to the apex of the gynostemium but ceases at the point of the insertion level of the perianth. Thus, in one and the same "floral tube" (as designated by Wilson and Just, 1939) of orchids, different degrees of adnation are seen, the ovary proper containing the fused vascular traces of all of the floral whorls and the gynostemium proper in which the individual traces of the stamens and stigmas are embedded.

Stamens. Robert Brown (1831) was the first to state in clear terms that the stamens in the orchid flowers are arranged in two alternating whorls, each whorl containing three stamens. Since then Darwin's investigations (1899) on several other orchids have brought to light a certain amount of evidence to support Brown's views. But as Darwin also believed that the lateral stamens of the outer whorl were fused with the labellum, he contemplated that only the lateral stamens belonging to the inner whorl were always present in the gynostemium.

It is not so easy to determine which particular trace represents which particular stamen just by observing a section of the gynostemium. "Compound" staminal traces have been demonstrated in the present study as a very common condition in orchid flowers. Some other salient points concerning the vascular supply to the stamens may now be recalled:

(1) In the Cypripedilinae, a1 and a2 are normally present and are functional. A1 is transformed into a staminode. In teratological flowers (see Worsdell, 1916)

sometimes A 2 or A 3 or even a3 may be represented by the corresponding staminodal outgrowths externally or by vascular traces internally.

(2) In the Ophrydinae it has been shown here that A 1 alone manifests itself as the functional stamen and that no other stamens are represented even by vascular traces.

(3) In the remainder of the members of the Monandrae, as a rule, A 1 is the functional stamen, a1 and a2 or sometimes A 2 and A 3, being present as traces. The origin and course of the various staminal traces (excepting the one pertaining to A 1) may be somewhat irregular in some advanced genera. They may be quite clear in the juvenile condition of the flower but later become obliterated, or they may be "compound" from the very beginning. In the majority of the genera, however, all of the four lateral stamens are represented by the "compound" traces, a1+A 2 and a2+A 3.

(4) The expression of a3, though rare, can still be seen in some instances.

The above facts, when considered from an "over-all" point of view, account for the presence of all of the six stamens belonging to the two whorls. At one time, perhaps, all of the six stamens were functional. During phylogenetic specialization, the median one of the inner whorl (a3) disappeared early, probably in correlation with the differentiation of the labellum. Subsequently, the elimination of the lateral stamens of the outer whorl was effected first and of the inner whorl later; this is suggested by the more frequent predominance of the latter and the less frequent expression of the former among the orchids here studied. However, when the vascular traces of the lateral stamens of both the whorls are present, they form "compound" traces as a1+A 2 and a2+A 3.

A study of the published floral diagrams of *Neuwiedia* (Pfitzer, 1889) reveals that an early step in the suppression of the three stamens of the posterior half of the flower (A 2, a3 and A 3) had already started here; hence the functional stamens were the median one of the outer whorl (A 1) and the lateral stamens of the inner whorl (a1 and a2). Such flowers specialized further along two distinct lines: (1) suppression of the median stamen of the outer whorl (A 1), which tendency gave rise to forms like the diandrous orchids, and (2) suppression of the lateral stamens of the inner whorl (a1 and a2) which tendency resulted in monandrous orchids. Such an interpretation is in conformity with the stand taken by Rolfe (1909–12). (These aspects are fully discussed in my paper, "Embryological studies in the Orchidaceae, Part II," which is under publication).

Carpel. According to the classical view, the orchid ovary is unilocular and tricarpellary; the ovules are marginal, the margins of the adjacent carpels having fused to such an extent as to obliterate the double nature of the ovule-bearing vascular traces. The median trace of each carpel supplies the respective stigma.

The only opposition to the above-mentioned view is that advanced by Saunders (1923, 1937). She contends that each of the main vascular traces of the ovary represents a carpel; that the main traces underlying the outer whorl of perianth are to be considered as solid sterile carpels bearing stigmas and that the main traces underlying the inner whorl of perianth members are to be considered as representing semi-solid carpels where placentae have approached the median trace of the carpel.

There is absolutely no anatomical evidence to favor Saunders' views. The inconsistencies and irrelevancies of the theory of "Carpel Polymorphism" have been

brought to light repeatedly by several workers in several plant families. So it becomes unnecessary to consider Saunders' attack with any seriousness.

However, one difficulty that may be postulated against favoring the classical view of the orchid carpel is that of the irregularity of the origin and differentiation of the median and marginal traces of each carpel. But this objection, if it can really be called an objection, will be nullified when we take into consideration the high degree of anastomoses, cohesion, adnation and other allied phenomena accompanying the structural evolution of the flower.

Summary

The orchid ovary is traversed by six main vascular traces. In the Cypripedilinae, the origin and subsequent development of these six traces are not attended by any secondary modifications. But among the monandrous genera, a series of increasingly complex and diverse patterns is witnessed; thus the number of vascular bundles that enter into the construction of the flower from the inflorescence axis is usually three, but this may be reduced to two; their method of breaking up into the six main traces of the ovary also is highly diverse in different genera. None of the main traces of the ovary show any signs of supply either to the placentae or to the ovules. The main traces begin to break up and supply the other floral members only at the upper extremity of the ovary.

Depending largely upon the presence or absence, number and nature of the vascular traces supplying the stamens, three types of vasculature of orchid flowers are recognized: Type I, characterizing the Cypripedilinae, Type II, characterizing the Ophrydinae and Type III, characterizing the rest of the Monandrae.

It is Type III that presents an interesting series of increasing complexity. The latter is intimately associated with anastomoses, cohesion and adnation of the individual vascular traces of the flower. The increasing trend of complexity of perianth members is seen in the derivation of marginal traces of the perianth members of one whorl from those of the other and their anastomoses. As a result of this, the places of origin of the staminal traces become highly displaced and carried to higher levels, until the adjacently placed lateral staminal traces form "compound" traces, here designated as a1 +A 2 and a2 +A 3. The effect of adnation on the different whorls of the flower has been described in detail.

The inferior ovary is looked upon as due to an extreme adnation of the different floral whorls. The outer and inner whorls of the perianth, though externally distinct from one another, present the same anatomical features and on this account the inner whorl is considered to be more sepaline than otherwise. The labellum is also shown to receive the same vascular supply as the rest of the perianth members; it is stressed that there is no evidence to consider it to be a compound structure, as was thought by Brown and Darwin.

The two lateral stamens of the outer whorl which were thought by Darwin to have fused with the labellum, are here shown to be represented in the gynostemium, either as individual traces (A 2 and A 3) or in their "compound" manifestations (a1 +A 2 and a2+A 3), whenever they are present. It has also been shown that the median stamen of the inner whorl is capable of expressing itself occasionally.

It is suggested that in the ancestral orchid flower all of the six stamens were functional; that in course of time the posterior three ceased to be functional and that it seems as if such a progenitor may have given rise to the

Diandrae on the one hand and the Monandrae on the other.

Evidence is presented in favor of the appendicular theory of the gynostemium, in opposition to the views of those who consider it to be a prolongation of the floral axis.

I am very thankful to Professor R. H. Wetmore for kindly reading the manuscript and offering valuable suggestions for improvement in presentation.

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BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, OCTOBER 20, 1948 VOL. 13, NO. 5

STUDIES IN THE GENUS HEVEA II

BY

RICHARD EVANS SCHULTES[1]

THE REDISCOVERY OF HEVEA RIGIDIFOLIA

IN 1852, Richard Spruce made the type collection of the extraordinary *Hevea rigidifolia* near the confluence of the Rios Uaupés[2] and Negro in the Amazonas of Brazil. Nearly a century has passed since this achievement, but, apparently until recently, no other collection has been made, and the species has remained known solely from the information derived from a study of the type material.

In March, 1944, during an extensive cytogeographic survey carried out in the Amazon Valley for the United States Department of Agriculture and in collaboration with the Instituto Agronômico do Norte, Dr. John T. Baldwin, Jr. discovered *Hevea rigidifolia* and introduced it into cultivation at Belém do Pará.

In 1945, Felisberto Camargo, director of the Instituto Agronômico do Norte, sent his botanical explorer, Senhor Ricardo de Lemos Fróes, to the upper Rio Negro

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[2] This river is known in Colombia as the Vaupés.

and lower Rio Uaupés area, where Spruce had collected so extensively, for an investigation of *Hevea* and several other genera of economic plants.

In July, 1946, in Belém, I had the pleasure of studying a number of the specimens of *Hevea* which Fróes collected on this trip and which Dr. Adolpho Ducke had determined (cf. Ducke in Bol. Téen. Instit. Agron. Norte no. 10 (1946) 13). The scope and quality of the collection are such that I am moved to compliment the collector most highly on his accomplishments and Dr. Camargo for his part in bringing about this valuable contribution to our knowledge of *Hevea* in one of the most isolated regions of the Amazon Valley.

Without a doubt the most outstanding achievement of Fróes' trip was his rediscovery of *Hevea rigidifolia*. Four excellent and extensive collections were made in three localities, all rather near the type locality. These collections greatly increase our understanding of this species which is certainly (with the possible exception of *Hevea microphylla* Ule (Schultes in Bot. Mus. Leafl. Harvard Univ. 13 (1947) 1–9) the most distinct of the whole genus. One of the collections includes several valves of the capsule and two seeds, both of which structures have hitherto been unknown; and another collection includes seedling material.

In May, 1947, Fróes recollected *Hevea rigidifolia* in sterile condition from a locality where he had found it two years previously. According to Senhor Fróes, two thousand seedlings of *Hevea rigidifolia* from this locality (Serra de Tumuhy) have been established at Belterra.

The Fróes collections of *Hevea rigidifolia* are important from several points of view. They indicate that the species is probably a very highly restricted endemic. It is evident also from a comparison of the collections with the type material that the species is apparently rather

stable, showing variations which are surprisingly slight for the genus. On the basis of a study of this new material, we can now attempt to discuss the relationships of *Hevea rigidifolia* with other species. Furthermore, the examination of the Fróes material has convinced me more firmly than ever that it is imperative to bring this species, which has a number of unusual characteristics found in no other species, into cultivation on a large scale for investigations in selection and hybridization and to study even more intensively its relationships.

There have been four descriptions of *Hevea rigidifolia*, including the original, but they have all been based on the type collection. The original description is very short and has proved to be inadequate, in view of the complications which are presenting themselves in the detailed and critical studies of the genus as to its subspecific concepts and phylogenetical relationships. The second[3] and third[4] descriptions, those of Mueller-Argoviensis, are

[3] "**. . . . foliolis coriaceis margine recurvis, alabastris masc. cylindrico-conicis angustis, calycibus pro 2/3 longitudinis partitis, laciniis triangulari-lanceolatis acute acuminatis, disci masc. glandulis lanceolato-subulatis glabris, antheris 6–10 irregulariter biseriatim verticillatis, columna supra-staminali integra glabra, stigmatibus breviuscule stipitatis . . . Arbor 30-pedalis. Foliola circ. 9–12 cm. longa, 4–5 cm. lata, lanceolato-elliptica, acute acuminata, basi acuta, subtus subglaucescentia, supra–laevigata, glabra, multo crassiora quam in congeneribus. Costae primariae crassae, secundariae tenuiores, subtus prominentes; venae validiusculae, subdeplanatae. Paniculae amplae, albido-v. cinereo-tomentellae. Calyces masc. aperientes 4 mm. aequantes v. paulo longiores, foeminei aperti usque 7 mm. longi, intus circa fundum minute subulato-glanduligeri; laciniae longe et anguste acuminatae.**"

[4] "**. . . foliolis coriaceis margine recurvis; alabastris masc. cylindrico-conicis angustis; calycibus pro 2/3 v. 3/5 longitudinis partitis, laciniis e base triangulari anguste lanceolatis acute acuminatis; disci masc. glandulis lanceolato-subulatis glabris; antheris 6–10 irregulariter biverticillatis, columna suprastaminali angusta glabra; stylo brevi distincto, ovario glabro.**

"**Arbor 30-pedalis. Petioli validi, foliola aequantes v. iis longiores,**

greatly amplified from the original of Spruce and have served until the present time; the third (1874) was reproduced with only slight alterations by Pax.[5]

In the following notes, I have thought it advisable to offer a new description, based upon the three previous ones, but extended and altered to conform with the additional information resulting from further observations and studies of the typical material and from an examination of the Baldwin and Fróes collections. The fact that it has been necessary to make only minor changes is at once a tribute to the accurate work of Spruce, Mueller-Argoviensis and Pax on the type collection and an indication of the unusual stability of this species-concept.

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apice valide biglandulosi. FOLIOLA circ. 9–12 cm. longa, 4–5 cm. lata, oblongato-elliptica, acute cuspidato-acuminata, basi acuta, rigidiora quam vulgo in genere, supra laevigata et nitida, utraque pagina glabra, subtus e glaucescente palliodora et validiuscule venulosa, venae vix prominentes; costae majores utroque latere circ. 12, primariae validae et valde prominentes. PANICULAE amplae, floribundae, micranthae, cinereo v. fere albo-tomentellae. CALYCES masc. aperientes 4 mm. aequantes v. paulo longiores, feminei aperti usque 7 mm. longi, utriusque sexus intus inferne praesertim vellereo-tomentelli. GLANDULAE disci florum masc. elongatae, erecto-patulae, acuminatae, basi tantum connatae et more ovarii et columnae suprastaminalis omnino glabrae. OVARIUM ovoideum, stylo brevi stigmatibus paulo longiore valido terminatum, teres et laeve, glaberrimum. Fructus ignoti."

[5] "Arbor ad 10 m. alta. Petiolus validus, foliola aequans vel superans, apice valide biglandulosus; foliola 9–12 cm. longa, 4–5 cm. lata, oblongo-elliptica, cuspidato-acuminata, basi acuta, valde coriacea, margine revoluta, supra laevia et nitida, utraque pagina glabra, subtus glaucescenti-pallida, valide venulosa; costae utroque latere ca. 12. Paniculae amplae, floribundae, cinereo- vel albo-tomentellae. Alabastra ♂ cylindrico-conica, angusta. Calyx ♂ 4 mm. longus, ♀ 7 mm. longus, utriusque sexus intus tomentellus; lobi triangulares, acuminati; disci glandulae ♂ lanceolato-subulatae, glabrae, acuminatae, basi tantum connatae; antherae 9–10, irregulariter biverticillata; columna staminalis glabra, ultra antheras longius producta; ovarium glabrum; stylus brevis. Fructus ignoti."

Hevea rigidifolia (*Spruce ex Bentham*) *Mueller-Argoviensis* in Linnaea 34 (1865) 203; in DC. Prodr. 15, pt. 2 (1866) 718; in Martius Fl. Brasil. 11, pt. 2 (1874) 300—Hemsley in Hooker's Icon. Pl. 26 (1898) t. 2573, figs. 11, 12, 13—Pax in Engler Pflanzenr. IV, 147 (Heft 42) (1910) 124—Ducke in Arch. Instit. Biol. Veg. Rio Janeiro 2, no. 2 (1935) 235; in Bol. Téen. Instit. Agron. Norte no. 10 (1946) 13.

Siphonia rigidifolia Spruce ex Bentham in Hooker's Journ. Bot. 6 (1854) 371.

ORIGINAL DESCRIPTION:

"*S. rigidifolia*, Spruce, MS.; foliolis ellipticis crasso-coriaceis glabris, paniculis pulveraceo-tomentosis, calycibus subacuminatis, antheris 5–8 ad basin columnae irregulariter subverticillatis.—*Ramuli* glabrati. *Foliola* breviter petiolulata, 5 poll. longa, 2½ poll. lata, acute acuminata, margine recurva, basi cuneata, multo crassiora et rigidiora quam in caeteris speciebus, subtus punctis crebis albicantia. *Paniculae* pyramidatae, semipedales. *Flores* pallide flavi, masculi 2 lin., foeminei 3 lin. longi. *Antherae S. luteae.* Stylus evidentior.

"A milky tree of 30 feet in height, from the caatingas of the Rio Uaupés *R. Spruce.*"

EXTENDED DESCRIPTION:

Arbor parva usque ad triginta ped. alta, 3.5 ad 10 poll. in diametro, latice albo. *Petioli* robusti, 8–24 cm. (maxima pro parte 13–17 cm.) longi, 1–3 mm. in diametro, teretes, cortice glabro rubicundulo-brunneo vel stramineo-brunneo, tenuiter striati, basi leviter subcarnoso-dilatati, apice valide biglandulosi. *Petioluli* robustiores, 3–13 mm. (maxima pro parte 5–7 mm.) longi. *Foliola* valde reclinata, statu adulto valdissime coriacea (et multo rigidiora quam illa in genere vulgo visa), perfecte oblongato-elliptica vel saepe elongato-elliptica, basi cuneata vel saepe valde rotundata, apice acute cuspidato-acuminata, margine conspicue recurvata, 6–19.5 cm. (maxima pro parte 10–13 cm.) longa, 3.5–8.5 cm. (maxima pro parte 4.5–6.5 cm.) lata, supra laevigata, pallide cinereo-viridia,

EXPLANATION OF THE ILLUSTRATION

PLATE VIII. HEVEA RIGIDIFOLIA (*Spruce ex Benth.*) *Muell.-Arg.* 1, terminal branch with inflorescence, one third natural size. 2 and 3, staminate flowers, natural size. 4, stamen, one and one third times natural size. 5 and 7, seeds, one third natural size. 8 and 9, valves of the capsule, one third natural size. 10 and 11, ovary, two and two thirds times natural size. 12 and 13, pistillate flowers, one and one third times natural size.

Drawn by A. N. FERRAZ

Plate VIII

valde nitida, omnino glabra, infra glaucescenter pallidiora crebro-tessellatis punctis albicantia et validiuscule venulosa, costis subtus prominenter elevatis, glabris (specialiter primariis), secundariis utrinque duodecim ad quindecim. *Paniculae* amplae, elongatae, folia subaequantes, aliquid rigidae, floribundae, minute cinereo- vel fere albotomentellae. *Alabastra masculina* anguste et longe cylindrico-conica, valde acuminata, calycis segmentis apice valde et conspicue imbricatis contortisque; *feminea* multo majora, acuminata. *Calyces* pro genere satis crassiusculi, masculini aperientes 3.5–4.6 (plerumque 4) mm. longi, feminei 6–8 mm. longi, extus densissime albotomentelli, intus usualiter glabri sed raro vel apicem versus vel fundum versus parce minute pulveraceo-tomentelli, utroque sexu per 2/3 vel 3/5 longitudinis partem partiti, laciniis e basi triangulari anguste lanceolatis, apice acute acuminatis, marginibus integris involutis, pallide luteis; laciniarum florum femineorum apicibus valde retortis. *Antherae* plerumque sex (raro septem ad decem), irregulariter biverticillatae, parvae; columna suprastaminalis angusta, gracilis, glabra, usque ad 2 mm. ultra antheras producta. *Disci glandulae* florum masculinorum elongato-subulatae, erecto-patulae, glabrae, acuminatae, basi aliquid connatae; florum femineorum magnae, irregulariter elongato-linguiformes, usque ad 1 vel 1.2 mm. longae, valde erectae, glabrae. Ovarium ovoideum, 1 mm. $\times$1.5 mm., glaberrimum sed nunc minute punctulatum, brevi cum stylo stigmatibus; stigmata congesta, subglobosa, crasso-conflata, glabra. *Coccorum valvae* lignosae, usque ad 5 cm. longae, 1.7–2 cm. latae; epicarpium tenue sed probabiliter vivo fibroso-striatum; endocarpium 2 mm. crassum, sicco valde contortum. *Semina* regulariter elliptico-ovoidea, valde angulosa, aureo-brunnea cum maculis irregularibus magnisque, ferrugineo-brunneis, 2.5–2.9 cm. $\times$1.6–1.9 cm. $\times$1.8–2.2 cm., raph-

ide prominenti et faciebus satis amplis. In terris saxosis, semi-xerophyticis, in plantarum societate quae in lingua brasiliense "caatinga" nominatur, in locis usque ad circa mille pedes altitudine crescit. Nomen vulgare "seringueira" vel "seringueira da serra" est.

COLLECTIONES EXAMINATAE:

BRAZIL: Estado do Amazonas, prope Panuré [Ipanoré] ad Rio Uaupés, Oct. 1852–Jan. 1853, *Richard Spruce 2527* (TYPE COLLECTION).

BRAZIL: Estado do Amazonas, Jauareté, Uaupés, Rio Negro. "Árvore de 9 m., 25 cm. [diam.]; folhas coriaceas, um tanto pendentes. "Seringueira." Oct. 22, 1945, *Ricardo de Lemos Fróes 21253*.

BRAZIL: Estado do Amazonas, Iraruca, Rio Içana. "Árvore, 7 m., 15 cm. [diam.]. Casca fina, latex branco, abundante, coagulavel. Folhas pendentes, coriaceas." Nov. 16, 1945, *Ricardo de Lemos Fróes 21394*.

BRAZIL: Estado do Amazonas, adjacencias da serra de Tunuhy, estando-se até a 308 metros de altitude. "Rica em látex branco, coagulavel." Nov. 14, 1945, *Ricardo de Lemos Fróes 21401*.

BRAZIL: Estado do Amazonas, Serra Tunuhy, [Rio] Içana, Rio Negro. May 5, 1947, *Ricardo de Lemos Fróes 22303*.

BRAZIL: Estado do Pará, Belém do Pará. "Seedling *cultivated* in Instituto Agronômico do Norte, collected by J. T. Baldwin, Jr., at Montepelago, Rio Uaupés, Estado do Amazonas, March 1944. Sterile." August, 1947, *Richard Evans Schultes 8663*.

The distribution of Hevea rigidifolia

The small number of stations now known for *Hevea rigidifolia* indicate that it is, with all probability, a highly restricted endemic, for the rather extensive collections of *Hevea* which have been made in other regions[6] in the Amazon Valley have never yielded this species.

Hevea rigidifolia appears to be centered near the confluence of the Rio Negro with the Río Vaupés, or, more precisely, in the triangular sector formed by the lower course of the Río Vaupés, the Rio Negro above its con-

[6] *Hevea rigidifolia* is erroneously attributed "am mittleren Orinoko" in Pflanzenr. IV. 147 (Heft 42) (1910) 124.

fluence with the Vaupés and the Colombian border. Since this species is endemic to caatingas, however, its dispersal is necessarily interrupted and usually confined to the hinterlands. Therefore, further explorations may and doubtlessly will increase our knowledge of its range. Inasmuch as the Fróes collections from Jauareté were made exactly on the Colombo-Brazilian boundary, it is safe to include *Hevea rigidifolia* in the enumeration of Colombian species of the genus (Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1945) 11). In 1945, I published the following remarks in this connection (here translated from the Spanish) (in Rev. Acad. Col. Ciénc. Exact. Físico. Nat. 6: nos. 22–23 (1945) 336): "This species, collected by the English botanist, Richard Spruce, in caatingas in the lower Vaupés near Panuré, Brazil, is represented in herbaria only by the type collection. The type locality at Panuré is very near the boundary between Colombia and Brazil and, for this reason, it seems probable that *Hevea rigidifolia* will also be found in the Vaupés of Colombia below Mitú."[7] It should be sought in the Río Querarí as well.

For the same reason, I suspect that in time we shall also be able to assign *Hevea rigidifolia* to the Venezuelan flora. It should be expected to occur in the general vicinity of the Piedra de Cocuy. Pittier (Manual de las plantas usuales de Venezuela (1926) 262) indicates that *Hevea rigidifolia* forms a part of the Venezuelan flora, but I strongly suspect that this statement is based upon collections of the very thick-coriaceous *Hevea pauciflora* (Spruce ex Bentham) Muell.-Arg. var. *coriacea* Ducke,

[7] In the small but critically interesting collection of *Hevea* which Paul H. Allen, of the Missouri Botanical Garden, made in this general area in 1943 and 1944 for the Rubber Development Corporation, *H. rigidifolia* is not represented. (See Baldwin in Amer. Journ. Bot. 34 (1947) 263 for reference to *Allen 3049*.)

frequent in the Orinoco area, which have been erroneously determined.

In spite of the fact that *Hevea rigidifolia* may probably occur within the boundaries of three different countries, I am of the opinion that, with the single exception of *H. minor* Hemsl., it represents the species which is most narrowly restricted in range[8] and possibly one of the oldest of the genus.

It is of interest to note that *Hevea rigidifolia* is sometimes found on caatingas at relatively high elevations. The *Fróes 21401* collection from Serra de Tunuhy was made at an altitude of approximately one thousand feet above sea level. I have found that in the peculiar habitat of the caatinga flora of these open sandstone mesas or campinas in the adjacent areas of Colombia, the greater the altitude above the forest floor the more intense the conditions of and response to xerophytism. Thus, the higher one finds the diminutive xerophytic *Hevea nitida* Mart. ex Muell.-Arg. var. *toxicodendroides* (R. E. Schultes et Vinton) R. E. Schultes (in Bot. Mus. Leafl. Harvard Univ., 13 (1947) 9–11), the more reduced it is in all its vegetative parts. It is significant that the specimens in *Fróes 21401*, from a tree growing so high above the jungle surroundings, shows no special vegetative adaptations correlated with increased intensity of heat, radiation, drought or other xerophytic conditions.

According to Senhor Fróes, *Hevea rigidifolia* is found on the flat sandstone mesas as well as on the lightly forested slopes formed by the talus from the eroded cliffs of the hills. The collection *Fróes 21401* was made in the light "talus-forest" of Serra de Tunuhy, the tree grow-

[8] The range of *Hevea camporum* Ducke, the specific status of which is now under question by Dr. Adolpho Ducke (in Bol. Técn. Inst. Agron. Norte no. 10 (1946) 19), is not known but may be less extensive than that of any other.

FIG. 12. Map showing the known range of HEVEA RIGIDIFOLIA (*Spruce ex Benth.*) *Muell.-Arg.*

ing in gravel and among huge, scattered blocks under severe conditions of chersophytic drought. Senhor Fróes described the habitat to me as follows: "*Hevea rigidifolia* in this locality (Serra de Tunuhy) is fair-sized because it is under a light forest; the crown of the slender *Hevea* protrudes above the forest seeking light. . . . I estimate that the mesa-like top of Tunuhy is 1000 feet above the forest floor, but I ascended only about 600 feet, where I collected number *21401*."

Variability of Hevea rigidifolia

The present study of the variability of important specific characters of *Hevea rigidifolia* is based upon an examination of: (1) the type and a duplicate type in the Royal Botanic Gardens at Kew; (2) a photograph of a specimen of the type collection from the Delessert Herbarium; (3) one duplicate type preserved in each of the following institutions: Gray Herbarium of Harvard University; the New York Botanical Garden; the British Museum of Natural History; the Fielding Herbarium at Oxford University; the Herbarium at Cambridge University, and the Herbarium Amazonicum Musei Paraensis (Museu Goeldi) in Belém do Pará; (4) thirty-six specimens of the four Fróes collections; (5) a young individual introduced to cultivation at the Instituto Agronômico do Norte by Baldwin in 1944. Furthermore, I have also had the opportunity of questioning Senhor Fróes in great detail about the habit and habitat of the trees from which his collections were made.

It is clearly apparent from a study of these collections from five different localities that *Hevea rigidifolia* is an exceptionally stable species. It is indeed unusual to find a concept of such stability in this very variable genus. Unless later investigations with large quantities of seed

should indicate otherwise, there seem to be no varieties or forms of the concept, a condition which does not appear to exist in any other well-known species with the possible exception of *H. microphylla*. All of the collections indicate that *Hevea rigidifolia* is a small tree, usually between twenty and thirty feet in height. However, there is apparently considerable variation in the diameter of the trunk which may measure, according to Fróes, from eight to twenty-five centimeters; this variability in the size of the trunk is found in a large number of small trees which grow under the xerophytic conditions of caatingas.

The leaflets of *Hevea rigidifolia* are apparently always of the same consistency, color and glaucescence; their adult size is very constant, varying usually from 10 to 13 cm. in length and 4.5 to 6.5 cm. in width; they are always peculiarly and strongly recurved-marginate; their tips are consistently long and sharply cuspidate-acuminate; there is never any trace of pilosity in the axils of the nerves; the number of secondary nerves is twelve to fifteen. Occasionally (as in *Fróes 21394*) the strongly rounded base of the leaflets departs from the cuneate condition which is usual in this species; this is, curiously enough, the only vegetative variation of importance which was noted, except for a very slight divergence from a perfectly oblongate-elliptic shape (as in some specimens of *Fróes 21253*).

The inflorescences in all of the collections are peculiarly rigid, are profusely flowered, and are more or less equal or subequal to the leaves.

No variations of any sort in the form of the staminate buds is apparent; all are very strongly cylindric-conic, conspicuously acuminate, and densely clothed with a white indumentum. The pistillate flowers, with the spreading and sharply recurved narrow acuminate tips

of the calyx lobes, show no variation. Size in the flowers is also constant.

I have studied five staminate flowers from various specimens of the type collection and thirty-six, taken at random, from the Fróes collections. The number of anthers is extremely constant, being six in all cases but two. In these cases seven anthers were found, the unusual insertion of an extra anther indicating abnormality. I am at a loss to explain Mueller-Argoviensis' statement that the number can vary between six and ten, unless a rare or abnormal condition existed in the material which he studied (necessarily material of the type collection). Hemsley (in Hooker's Icon. Pl. 26 (1898) t. 2573, fig. 11) indicated six anthers, irregularly inserted in two verticils. Spruce, in the original description, described them as they are in *Hevea guianensis* Aubl. var. *lutea* (Benth.) Ducke & Schultes, which has most frequently five, less frequently six, but rarely (and probably abnormally) seven or eight. It is evident from a study of the new collections that the number of stamens is normally and quite constantly six.

No variation of any appreciable degree was noted in the size, shape, and insertion of the lobes of the staminate disk. In all of the flowers examined, they are large, very long-acuminate, and conspicuously spreading. It is of interest to note that the disk lobes in *Hevea rigidifolia* are larger than in any other species.

An examination of three pistillate flowers from the duplicate type at the Gray Herbarium, two from the type at Kew, and fifteen from the several Fróes collections has served to emphasize the stability of all the important characters, with the exception of the indumentum of the inner surface of the calyx. The calyx lobes are invariably divided about two thirds or three fifths of their length; the tomentulose indumentum of the exterior of the calyx

lobes is surprisingly constant in density; the interior of the lobes is almost always perfectly glabrous; the ovary is completely glabrous, sometimes very slightly punctate; the style is very much abbreviated and thickened; the stigma lobes are unusually large and carnose, covering the short style; the annular disk is consistently very large and conspicuous, very irregularly deep-laciniate, the tongue-shaped segments often up to 1 or 1.2 mm. in length—probably the largest of any species of *Hevea*.

All but three of the pistillate flowers which I examined were completely glabrous within. In the three exceptions, I found an extremely sparse tomentulose indumentum on the *upper half* of the inner surface of the calyx, especially near the apex of the lobes. Seibert (in Ann. Mo. Bot. Gard. 34 (1947) 341, pl. 38), has illustrated the pistillate calyx as very remotely tomentulose on the upper half of its interior surface. Hemsley (loc. cit. fig. 12) published a drawing of an open pistillate calyx of *Hevea rigidifolia* showing a tomentulose condition on the entire inner surface of the lobes, but this was an error. I have examined the original sketch which is attached to the type sheet at Kew and have found that the interior surface of the pistillate calyx is drawn as tomentulose *only near the apex* of the lobes. The dissected flower on which this sketch was based agrees with the original drawing. It should be noted that the original sketch of *Hevea rigidifolia* was redrawn and, unfortunately, altered in preparing the plates for publication.

Mueller-Argoviensis (in Martius Fl. Brasil. 11, pt. 2 (1874) 300) stated that the calyces of both staminate and pistillate flowers are "intus inferne praesertim vellereo-tomentelli."[9] Pax (in Engler Pflanzenr. 4, 147 (Heft 42)

[9] In an earlier description of *Hevea rigidifolia*, Mueller-Argoviensis (in DC. Prodr. 15, pt. 2 (1866) 718) indicated that the pistillate calyx was "intus circa fundum minute subulato-glanduligeri." (See footnote 3.)

(1910) 124) repeated this, stating: "calyx. . . . utriusque sexus intus tomentellus." I find it difficult to reconcile this with my own observations on flowers from both the type and from the new material, but I think we may be justified in assuming that there is some variability in this character and that the normal condition is a glabrous interior of the pistillate calyx.

Hemsley (loc. cit. fig. 13) has also published a sketch of the ovary showing a sericeous indumentum covering all parts of the ovary. Mueller-Argoviensis (loc. cit.) and Pax (loc. cit.) both indicate "ovarium glabrum"; this coincides with my own observations.

Relationships of Hevea rigidifolia

There has been some difference of opinion with regard to the closest affinities of *Hevea rigidifolia*. Mueller-Argoviensis, in his description of *Hevea nitida*, wrote: "evidenter affinis *H. rigidifoliae* et *H. brasiliensis*." In a detailed consideration of generic subdivisions in *Hevea*, Huber (in Bol. Mus. Paraense 4 (1906) 622, 632) included *Hevea rigidifolia* in the section *Bisiphonia*, series *Luteae*, together with *H. lutea* (Benth.) Muell.-Arg.,[10] *H. cuneata* Hub.,[11] *H. Duckei* Hub.,[12] *H. paludosa* Ule, *H. apiculata* Baillon[13] and *H. Benthamiana* Muell.-Arg.

Huber's statements regarding the relationships of *Hevea rigidifolia* should be of interest because of his vast knowledge of the genus, although it is probably true that, due to his confusion of an unusual variant of *H. Benthamiana* from the Rio Negro with *H. rigidifolia*,

[10] Now considered to represent *Hevea guianensis* var. *lutea*.

[11] A poorly understood concept representing possibly a form of *Hevea guianensis*.

[12] Now included by Ducke as a synonym of *Hevea Benthamiana*.

[13] Probably a variant of *Hevea guianensis*.

he did not, at that time, clearly delimit the former from the latter species. He wrote (loc. cit. 632), translated: "Pertaining undoubtedly to the *Luteae* series because of the disposition of the anthers, *Hevea rigidifolia* occupies, from other points of view, a special position in this group .... In its whitish pubescence and acuminate staminate buds, the inflorescence strongly suggests *Hevea brasiliensis* (HBK.) Muell.-Arg. Furthermore, the segments of the disk of the staminate flower are more strongly developed in this species [i.e. *H. rigidifolia*] than in any other species." Later, the same investigator (in Bol. Mus. Paraense 7 (1913) 202) indicated that the position of *Hevea rigidifolia* in the *Luteae* series was open to some doubt; and (loc. cit. 206) that it might be necessary to remove *H. microphylla* Ule[14] and *H. minor* from series *Intermediae* (he considered series *Luteae* and *Intermediae* to represent provisional classifications and not natural groups) and, together with *H. rigidifolia*, form a new group which would be characterized by a strong development of the segments of the staminate disk.

Ducke more recently stated (in Arch. Instit. Biol. Veg. Rio Janeiro 2, no. 2 (1935) 235): "According to the descriptions, the specie [i.e.: *Hevea rigidifolia*] differs from *H. Benthamiana* principally by its glabrous rigid coriaceous leaflets with recurvate margin; the discus and the anthers (6 to 10) do not seem to differ in any essential character from those of the typical *Benthamiana*." After having had occasion to see the Fróes material, Ducke (in Bol. Téen. Instit. Agron. Norte no. 10 (1946) 13) wrote in regard to *Hevea rigidifolia* "distinguese, de uma *Benthamiana* de folhas inteiramente glabras, pela consistencia rigidamente coriacea das mesmas. . . . as flores masculinas são mais longamente acuminadas e

[14] Until recently confused with *Hevea minor*.

mais estreitas que em qualquer especimen de *Benthamiana*, por mim visto."

The extensive Fróes material, with its abundance of flowers, enables us to evaluate more critically and more extensively than has hitherto been possible the relationships of *Hevea rigidifolia*. It would appear quite probable that *Hevea rigidifolia* occupies a somewhat intermediate position between *Hevea pauciflora* var. *coriacea*[15] and *H. Benthamiana*,[16] having, florally at least, closer affinities with the latter than with the former.

The extremely heavy coriaceous nature and the glaucescence of the leaflets of *Hevea rigidifolia* as well as the glabrous condition of the lower surface of the leaflets

[15] In the present article, I am using the concept *Hevea pauciflora* var. *coriacea* in the sense in which it has been established and used by Ducke (in Arch. Instit. Biol. Veg. Rio Janeiro 2, no. 2 (1935) 239). The concept has also been used in this sense in several of my previous papers (in Bot. Mus. Leafl. Harvard Univ. 12 (1945) 1–32; in Rev. Acad. Colomb. Ciénc. Exact. Físico-Quím. Nat. 6, no. 22–23 (1945) 331–338; in Rev. Fac. Nac. Agron. (Medellín) 6, no. 22 (1946) 18–45). I suspect that what has been considered as *Hevea pauciflora* var. *coriacea* represents a concept deserving varietal distinction. Baldwin calls this *H. confusa* (Baldwin: in Journ. Hered. 38 (1947) 54; Baldwin & Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1947) 335). Until it is possible to investigate the entire *Hevea pauciflora* complex critically, however, I believe it is advisable to maintain Ducke's treatment of it. A complete study of the *H. pauciflora* var. *coriacea*—*H. rigidifolia*—*H. nitida*—*H. confusa* problem and of the relationships between these concepts is urgently needed and must be carried out before a clear understanding of the genus as a whole can be expected. Ducke has recently (in Bol. Técn. Instit. Agron. Norte no. 10) (1946) 18) indicated doubt as to whether *Hevea confusa* should be maintained as a variety of *H. pauciflora* or incorporated with *H. pauciflora* var. *coriacea*.

[16] The writer believes that *Hevea Benthamiana* and *H. Spruceana* (Benth.) Muell.-Arg. are distantly allied species and that some relationship could, therefore, be expected to exist between *H. rigidifolia* and *H. Spruceana*. Since it appears, however, to be of a minor degree, a detailed analysis of this relationship will not be discussed in the present study.

combine with other general similarities in vegetative characters to indicate a rather close relationship with its companion of the caatingas, *H. pauciflora* var. *coriacea*. It is worth pointing out, incidentally, that while coriaceous leaflets are very possibly a manifestation of xerophytic caatinga conditions in both of these species, as in many other plants, there are sufficient similarities in vegetative characters to indicate that this is due to some affinity and not to an ecological parallelism between *Hevea rigidifolia* and *H. pauciflora* var. *coriacea*.

The seed of *Hevea rigidifolia* does not appear to be similar to that of *H. pauciflora* var. *coriacea*. It is larger, broader in relation to its length, and much less sharply angular. However, one seed preserved with the collection *Fróes 21253* curiously approaches the shape and size which, so far as we know, is usual for *Hevea pauciflora* var. *coriacea*, being smaller, narrower, and very sharply angular in cross section. (This seed may have been included erroneously in *Fróes 21253*, because it does not match any other seeds in the same collection. Furthermore, *Fróes 21253* was growing in close proximity to *Fróes 21249* which appears to be referable to the *Hevea pauciflora* var. *coriacea* complex, and a confusion as to the source of this seed would not be difficult.) Ducke (in Bol. Téen. Instit. Agron. Norte no. 10 (1946) 13) indicates that the seed of *Hevea rigidifolia* is similar in shape and size to that of typical *H. pauciflora*. If this unique seed actually belongs to *Hevea rigidifolia*, it might suggest some relationship with *H. guianensis* var. *lutea* or *H. nitida* which have similar angular seeds. We cannot draw any definite conclusions, however, on the basis of the few known seeds of *Hevea rigidifolia*.

In floral characters, however, there is less to point to a close affinity between *Hevea rigidifolia* and *H. pauciflora* var. *coriacea*. This is especially true when the dif-

ferences in such critical characters as the number of stamens, the size of the anthers, the length of the suprastaminal column, the size and form of the glandular lobes in the staminate flower, and the condition of the annular disk in the pistillate flower are taken into consideration. The very different form of the masculine buds—short, obtuse, even somewhat truncate in *Hevea pauciflora* var. *coriacea*, but extremely long and acuminate with the tips of the segments peculiarly spiral-imbricate in *H. rigidifolia*—likewise would tend to indicate that the affinity between the two might not be exceptionally close.

The young leaflets and seedling leaves of *Hevea rigidifolia*, as in some specimens of *Fróes 21253*, are strikingly similar to the adult leaflets of *H. pauciflora* var. *coriacea*, although the shape and size of the adult leaflets of *H. rigidifolia* are peculiar and cannot be easily confused with those of any other species.

In connection with the relationship of *Hevea rigidifolia* and *H. pauciflora* var. *coriacea*, it is pertinent to discuss several interesting collections which, in some respects, would superficially appear to be rather intermediate between the two concepts. As stated above, in March, 1944, Dr. John T. Baldwin, Jr. discovered *H. rigidifolia* and introduced it into cultivation (Baldwin in Am. Journ. Bot. 33 (1946) 215–216). There is one young individual growing vigorously in the collection at the Instituto Agronômico do Norte (Pl. IX).

Baldwin made chromosome studies in the field and prepared herbarium material, but unfortunately there appears to be some confusion in the determination of several of his herbarium collections. In two articles (Journ. Hered. 38 (1947) 59; Am. Journ. Bot. 34 (1947) 261) Baldwin cites his collections *3669* and *3670* as representing *Hevea rigidifolia*. I have studied a specimen of *Baldwin 3670* which is preserved in the Herbarium of

the Arnold Arboretum. It clearly represents one of the numerous variants of *Hevea pauciflora*. A good photograph of *Baldwin 3669*, a specimen of which I have not seen, has been published (in Am. Journ. Bot. 34 (1947) 264, fig. 2). It represents the same variant of the *Hevea pauciflora* complex as *Baldwin 3670*. Although these collections, with fruit but lacking flowers, exhibit similarities in certain characters with typical *Hevea rigidifolia*, it is highly inadvisable, in my opinion, to consider them as representing this peculiarly distinct species.

Several valves of the capsule which accompany *Baldwin 3670* would appear to be typical of *Hevea rigidifolia* in the shape and size of the few seeds, for both approach somewhat the analagous fruiting material of *Fróes 21253*. The ligneous valves of *Hevea rigidifolia* are peculiar to that species, being large, long and narrow with unusually thick endocarp, and very strongly twisted due to the explosive opening of the capsule; whereas in *Hevea pauciflora* var. *coriacea* the valves are smaller, as broad as long and have relatively thick and strong ligneous walls which are not in the least distorted during the explosive shedding of the seed. The pedunele of the fruit, preserved in *Baldwin 3670*, is like that of *Hevea rigidifolia*. However, it is in a study of the leaflets, so extraordinarily constant in typical *Hevea rigidifolia*, that doubts arise as to the real identity. Although the under surface of the leaflets of *Baldwin 3670* is armed with the minutely tessellate, waxy scales which lend the peculiar dull waxy-gray color to that part of the leaf of *Hevea rigidifolia*, the individual scale-like mosaic points are much smaller in the Baldwin collection than is normal for *Hevea rigidifolia*. It is, however, principally in the texture and general appearance of the leaflets that *Baldwin 3670* deviates most from typical *Hevea rigidifolia*. The leaflets are long and narrowly lanceolate-elliptic, departing from the very

characteristic and constant oblong-ovate shape; the tips do not have the very long and pronounced cuspidate acumen so typical of *Hevea rigidifolia;* the upper surface is, in life, apparently much duller and somewhat less glaucescent; the lower surface is not so whitish; the margin is very much less conspicuously inrolled; the petiolules are extremely abbreviated, whereas one of the major characteristics of *H. rigidifolia* is the presence of an unusually long petiolule; and the texture, in general, is far less coriaceous. The leaflets of *Baldwin 3670* are very close indeed in shape, size and texture to those of *Hevea pauciflora* var. *coriacea.*

Baldwin (in Journ. Hered. 38 (1947) 56) has stated that *Hevea pauciflora* "is probably the prototype of *H. brasiliensis* and was likely one of the parents of *H.rigidifolia.*" Later, the same investigator went much farther and wrote: (in Am. Journ. Bot. 34 (1947) 265) "... *H. rigidifolia* (and certain other species) may have originated from intergeneric hybridization of *Hevea* and *Cunuria.* For this hypothesis, *H. pauciflora* (from which it is considered that *H. brasiliensis* evolved) and *Cunuria crassipes* with purplish fruit are selected as possible parents." I cannot accept these assumptions for which no shred of evidence is advanced. Baldwin (loc. cit. 265) advances, apparently as arguments for his reasoning, a miscellany of observation and speculation when he states: "At Montepelago .... and at Iraruca .... purplish-fruited *Cunuria crassipes* grows adjacent to *H. rigidifolia.* The leaflets of this species of *Hevea* are cunurioid. On top of the hill at Montepelago, is a huge tree referable to *H. pauciflora,* and that tree is buttressed just as representatives of *Cunuria* are buttressed. Seed of *H. rigidifolia* and of *H. pauciflora* are much alike. Those of *H. confusa,* though smaller, fall in this group. Under influence of the elements, the seed of *H. rigidifolia* lose

their color pattern and assume the uniform brownish-red hue of *Cunuria* seed. That the natives recognize in the seed of *H. pauciflora* resemblance to those of *cunury* may be of significance."

Another very interesting collection is *Allen 3049* from the Río Papurí, an affluent of the Vaupés, which forms part of the Colombo-Brazilian boundary. The leaflets are somewhat like those of typical *Hevea rigidifolia*, but the seed and capsule valve suggest those of *H. pauciflora* var. *coriacea*. The seeds, smaller than usual for the *Hevea pauciflora* complex, are very strongly angular, and the valves, long in relation to their breadth, are not twisted. The leaflets, less coriaceous than in typical *Hevea rigidifolia*, are unusually obovate and very shortly cuspidate; they are extremely large. Of this collection Baldwin (in Am. Journ. Bot. 34 (1947) 263) writes: ". . . is a puzzling specimen. R. J. Seibert has annotated it as a possible hybrid of *H. pauciflora* (or *H. confusa*) and *H. rigidifolia* . . . carpels of old fruit, which seem referable to *H. confusa* Hemsl. and which could have been wrongly associated with the collection. . . . My inclination is to consider the material . . . . as *H. confusa* with influence from *H. rigidifolia*."

A third collection of significance in this problem is *Fróes 21249*. This likewise represents a variant of the *Hevea pauciflora* complex, but not the same variant as *Baldwin 3669*, *3670* and *Allen 3049*. This extensive collection has leaflets which suggest, in several minor characters, those of *Hevea rigidifolia*, but its flowers indicate its true affinities. Upon superficial examination of the leaves, I annotated this collection in July 1946 as *Hevea rigidifolia*, but later, detailed examination of the flowers disclosed my error. Baldwin (loc. cit. 263) has considered this collection to represent *Hevea rigidifolia*, stating: "*Fróes 21249* shows influence of *H. confusa*. This col-

lection and *Allen 3049* resemble certain of my specimens of *H. confusa* from along the Rio Negro." In May, 1947, he annotated two specimens in the Herbarium of the Instituto Agronômico do Norte (*16736*, *16737*) as "*H. rigidifolia* with influence from *H. confusa*." It is indeed of interest that *Fróes 21249* was found growing in close proximity to an individual of *Hevea rigidifolia* (*Fróes 21253*).

It is suggestive that some relationship may exist between *Hevea rigidifolia* and *H. nitida*. Baldwin (in Journ. Hered. 38 (1947) 59) considers *Hevea rigidifolia* "and *H. confusa* [*H. pauciflora* var. *coriacea*], *H. pauciflora* and *H. viridis* [*H. nitida*] to be expressions of the same complex." There is not only a similarity in the seed, but also the general coriaceous and reclinate condition of the leaflets could be interpreted as indicative of some degree of affinity. The floral characters of the two species, however, do not approach each other in any essential respect. The flowers of *Hevea nitida* indicate, in my opinion, a very close relationship with *H. brasiliensis*, thus removing *H. nitida* from any immediate phylogenetic proximity to *H. rigidifolia*.[17]

The resemblance of the seed of *Hevea rigidifolia* to that of one form of *H. brasiliensis* of the upper reaches of the Solimoes must be interpreted as coincidental. The "similarity" between the flowers of *Hevea rigidifolia* and *H. brasiliensis* which Mueller-Argoviensis intimated when he wrote in the description of the latter: "facies florum ut in *H. rigidifolia* sed structura diversa" is entirely superficial and, from a phylogenetic point of view, probably insignificant.

There does appear to be a likeness between the nor-

[17] Baldwin (loc. cit. 59) considers *H. pauciflora* var. *coriacea* (*H. confusa*) and *H. nitida* (*H. viridis*) so closely allied that they "may eventually be combined." I cannot subscribe to this opinion.

EXPLANATION OF THE ILLUSTRATION

PLATE IX. A seedling of HEVEA RIGIDIFOLIA (*Spruce ex Benth.*) *Muell.-Arg.*, growing in the garden of the Instituto Agronômico do Norte at Belém do Pará, Brazil.

Plate IX

mal seed of *Hevea guianensis* var. *lutea* and that of *H. rigidifolia*, especially in shape and in coloration. The seed of the former is, however, smaller than that of the latter. This similarity may be significant, but we cannot draw any definite conclusions on the basis of the few known seeds of *Hevea rigidifolia*.

The flower of *Hevea rigidifolia* does indeed show, in several characters, an approach to that of *H. guianensis* var. *lutea;* this was suggested by Spruce in the original description when he stated: "antherae *S. luteae.*" None of the floral characters, however, indicates any degree of close affinity. Moreover, the habits and habitats, and therefore probably also the history, of the two concepts are very unlike in all respects, for the one is a widely distributed forest giant growing on well-drained ground along the banks of rivulets or brooks, whereas the other, apparently a highly restricted endemic, is usually a small tree of xerophytic caatingas.

In floral characters, *Hevea rigidifolia* does, as Ducke has pointed out, resemble *H. Benthamiana* very closely. In *Hevea rigidifolia* the staminate buds are extremely acuminate and cylindric-conic; in *H. Benthamiana* they are commonly acuminate, although the latter does not have the segments apically spirally twisted as does the former. Although the flowers of the former are much larger than those of the latter, the general form of the urceolus of the staminate flower is markedly similar. There are, however, several rather important differences which do serve to separate the two. In *Hevea rigidifolia* the number of anthers, surprisingly constant, is very low (normally only six), the suprastaminal column is conspicuously slender and elongate, and the ovary is completely glabrous; whereas, in *H. Benthamiana*, the anther number is variable (usually from six to nine), the column is short, and the ovary is densely white-sericeous. In both

species, however, the lobes of the disk in the staminate flower are similar, being rather elongate, very acuminate and conspicuously erect-spreading. The lax and irregularly spreading long-acuminate tips of the calyx lobes of the female flower of *Hevea rigidifolia*, however, has no similarity to any of the forms of *H. Benthamiana* known to me; indeed, the female flower of *Hevea rigidifolia*, which, upon superficial observation would seem to be somewhat like that of *H. microphylla*, appears to be unique in the genus in this interesting characteristic.

The characters of the ligneous valves of the fruit have hitherto not been utilized taxonomically, but it is of great interest to note in passing that those of *Hevea rigidifolia* are very like those of most of the known forms of *H. Benthamiana* in having an unusually thin endocarp. The long and narrow shape of the valves of *Hevea rigidifolia* is very different from that which is commonly seen in *H. Benthamiana*, but it does remind one of the shape of the valves of *H. Spruceana*. Ducke (in Bol. Téen. Instit. Agron. Norte no. 10 (1946) 13-14) indicates that a specimen collected by him in 1905 on the Rio Negro at Barcellos and distributed by Huber as "*Hevea rigidifolia*" is a form of *H. Benthamiana* var. *subglabrifolia* Ducke with perfectly glabrous leaflets. (See also Ducke in Arch. Instit. Biol. Veg. 2, no. 2 (1935) 235 and in Arquiv. Serv. Florest. Rio de Janeiro 2, no. 1 (1943) 36.)

Recently in Belém, I had occasion to study a remarkable collection of *Hevea Benthamiana* from the Rio Negro which Ducke has determined as representing a perfectly glabrous form of var. *subglabrifolia*.[18] I believe that further study will possibly indicate that this collection represents a distinct variety. The reclinate leaflets

[18] Brazil: Amazonas, Rio Negro infer., loco Acajutuba. "Igapó secus rivulum ad marginem campinae. Arbor 18–20 m.; latex flavidus, parum copiosus." March 22, 1941, *Ducke 1963*.

are extremely coriaceous with strongly recurvate margins, as in *Hevea rigidifolia*, and although they are much smaller and more narrowly lanceolate-elliptic, they could very easily be misidentified (without fertile parts) as *H. rigidifolia*. The seeds and capsules of this collection, however, unquestionably belong to the concept *Hevea Benthamiana;* they are much smaller than in typical *Hevea Benthamiana*, but they are perfectly ovoid and are yellowish or light golden tan with large reddish brown or brownish black spots. The tree, eighteen or twenty meters tall, had sparse yellowish latex. It grew along a brooklet at the edge of a savanna. According to Ducke, the coriaceous character of the leaflets of this variant was gradually lost as one penetrated farther into the more densely forested igapó. This collection, as the analagous Barcellos material mentioned above, provides us with interesting data for a consideration of xerophytic parallelisms in *Hevea*. It is entirely possible, too, that this unusual form of *Hevea Benthamiana* which, at our present state of understanding, we call a parallelism, may be fundamentally significant as indicative of some actual relationship between *Hevea Benthamiana* and *H. rigidifolia*.

Possible economic and scientific importance of Hevea rigidifolia

Little is known of the economic value of *Hevea rigidifolia*. Ducke (in Rev. Bot. Appl. 9 (1929) 628) intimated that the species "semble fournir du caoutchouc," but naturally he could make no mention at that time as to whether or not it was ever exploited. Huber (in Bol. Mus. Paraense 4 (1906) 633) stated that *Hevea rigidifolia*: "foi designada ao Sr. Ducke como fornecendo borracha bôa," but this statement was made in reference to a collection from Barcellos which was misidentified as *H. rigidifolia* (Ducke loc. cit.). Jumelle ("Les plantes

a caoutchoue et a gutta" (1903) 132) repeated Huber's statement that *Hevea rigidifolia* yields a good rubber. La Rue (USDA Bull. 1422 (1926) 8) included *Hevea rigidifolia* in a list of species yielding "fair to good rubber," but there seems to be no basis for this statement. Spruce (in Hooker's Journ. Bot. ser. 3, no. 6 (1854) 371) merely remarked that it is "a milky tree of 30 feet."

Pittier (loc. cit.) enumerated three species of *Hevea* for the flora of Venezuela: *H. Benthamiana*, *H. minor* and *H. rigidifolia*, but, as stated above, it is doubtful that his report of the last-named species is based on correctly determined material; it refers probably to *H. paucifiora* var. *coriacea*. However this may be, Pittier writes that (translated) "of the three, the two first seem to give good rubber, but we know nothing about the third. It is probable that all take part in rubber production in the country."

The field data annotated on *Fróes 21394* indicate merely "latex branco, abundante, coagulavel," and *Fróes 21401* adds that the species can be "rica em latex branco, coagulavel."

In writing of several of his caatinga collections, Fróes ("Excursão botânica ao alto Rio Negro" Mss. report to Dr. Felisberto C. de Camargo (June 4, 1946) 23) states (translated): "The Heveas of the forest at Javarité (*21231*, *21249*, *21251*, *21253*) which are also common in the stretches of forest at Caiary-Aiary are low, measuring hardly 5 or 6 meters by 10 to 12 centimeters in diameter at breast height, with heavy and reclinate foliage, with medium-sized fruits as can be seen from the specimens collected in the region of the Rio Içana, in caatingas similar to those of Caiary-Aiary; they certainly must be little known because of the restriction of this species to its peculiar habitat. These forms of Hevea have, in themselves, no commercial importance because besides

their small size they are poor producers of latex, and the latex itself is of inferior quality. However, they would be of scientific value because of their rarity."

It would seem from this statement, and from others in the same report which indicate that the greater part of the upper Rio Negro production of rubber is from *Hevea Benthamiana*, that we are justified in inferring that *Hevea rigidifolia* furnishes none of the rubber produced in the area. This does not, however, assist in the appraisal of the quality of the rubber, for it is clear that the principal reason for not utilizing *Hevea rigidifolia* would be its small size. It might possibly be true that, as in the case of *Hevea nitida* var. *toxicodendroides*, its latex could be of high quality even though almost unobtainable due to the diminutiveness of the plant.

The fact that in its native state *Hevea rigidifolia* is of no commercial interest does not, however, indicate that it is devoid of importance to the scientific program of Hevea-investigation now in progress cooperatively between the United States Department of Agriculture and several Latin American countries. I consider that one of our most urgent tasks is the introduction of extensive living material of *Hevea rigidifolia* from several different localities to one or several of our experimental nurseries.

The differences between *Hevea rigidifolia* and the species commonly exploited, especially *H. brasiliensis*, are so great that we would be justified in expecting a number of interesting, and perhaps even revolutionizing, characteristics to appear as a result of an intensive program of selection and breeding.

This small tree is native to isolated sterile (cretaceous) sandstone caatingas on the pre-cambrian granitic Brazilian shield where the pH is probably rather highly acidic and where conditions of psammophytic and chersophytic drought prevail even during the rainy season. How this

species will react in growth as well as in quality and yield of latex when planted on a rich soil with an abundant availability of water is certain to be enlightening.[19] Selection should be carried out to some extent in the caatingas in order to secure for scientific study the most outstanding individuals from several points of view. A still more rigorous and accurate selection can be practiced in nurseries if large numbers of seedlings are planted and studied under controlled conditions. The potentialities of this species as a fast grower, outstanding yielder, disease-resistant strain, drought-resistant material, root-stock, crown-budding stock, as well as in numerous other respects, are certainly worth investigation.

The very fact that *Hevea rigidifolia* is one of the most distinct of the dozen or more species of the genus is indicative of the value which it might have in a plant-breeding program. This is especially true when one considers the possibilities which might arise as a result of chromosome incompatibility.

It is likewise imperative that we collect ample specimens of the coagulated latex from *Hevea rigidifolia* in its native state for chemical examination and later chemical comparison with latex from the same species cultivated under varying ecological conditions. It is possible that, as in the case of *Hevea nitida* in the igapós of the Vaupés of Colombia, of *H. Spruceana* and of *H. paucifiora* var. *coriacea*, the rubber of *Hevea rigidifolia*, of itself, will be of little or no commercial value. The rapid progress in the study of the synthetic elastomers, however, is creating a demand for rubbers of varying properties for use as "fillers" and the latex of no species of *Hevea* should be overlooked as a potential raw material for utilization in the synthetic rubber industry.

[19] The individual introduced by Baldwin in 1944 to Belém do Pará, planted on very light white sandy soil, exhibits an unusually slow growth. It is, at three years, only about five feet tall.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, NOVEMBER 24, 1948 VOL. 13, NO. 6

NOTES ON ORCHIDS OF THE AMERICAN TROPICS

BY

CHARLES SCHWEINFURTH

NEW CONCEPTS OF THE PANAMANIAN ORCHID FLORA

THE following new concepts became apparent in the course of the critical work undertaken by Mr. Paul H. Allen on the orchid flora of Panama.

Oakes-Amesia *C. Schweinfurth & P. H. Allen gen. nov.*

Divisio: Acrotonae. Tribus: Kerosphaereae. Series: Pleuranthae. Subtribus: Ornithocephaleae. Flores parvi. Perianthii partes liberae, late patentes. Sepala ovata vel oblongo-ovata, mucronata. Petala sepalis majora, late cuneata, apice truncata vel retusa. Labellum medio profunde trilobatum, per medium longitudinaliter tubulo percursum. Columna brevis, supra in processum rostellarem superne dilatatum et trilobulatum extensa. Anthera perlonga, sigmoidea, supra abrupte semigloboso-concava. Pollinia quattuor, parva, stipiti perlongo affixa.

Herba pusilla, epiphytica, *Ornithocephalo* valde affinis. Caulis perbrevis, foliorum circulo omnino obtectus. Folia equitantia, late patentia, infra vaginis imbricantibus articulata. Inflorescentiae racemosae, axillares, plurifforae, folia superantes.

Oakes-Amesia cryptantha *C. Schweinfurth & P. H. Allen sp. nov.*

Herba pusilla, epiphytica. Radices fibratae, pubescentes, numerosae. Caulis perbrevis, foliorum vaginis valde imbricatis omnino obtectus. Folia equitantia, vaginis articulata; laminae elliptico-lineares, acutae; vaginae conduplicatae. Inflorescentiae singulae vel tres, in foliorum superiorum axillis, racemosae, folia paulo excedentes. Flores parvi, cum segmentis liberis patentibus. Sepalum dorsale oblongo-ovatum, concavum, valde mucronatum. Sepala lateralia oblique ovata, concava, valde mucronata. Petala triangulari-cuneata, abrupte et late truncata vel leviter retusa. Labellum medio profunde trilobatum, valde concavum cum lobis lateralibus et lobi medii lateribus erectis; lobi laterales late oblongi, apice rotundati; lobus medius expansus subquadrato-cuneatus, apice truncatus; discus per medium tubulo percursus et supra tubulum fascia papillosa ornatus. Columna brevis, apoda, supra geniculata, antice cum processu rostellari elongato trilobato. Anthera operculata, incumbens. Pollinia quattuor.

Plant epiphytic, small, up to 5 cm. high. Roots slender, fibrous, finely pubescent, numerous. Stem obscure, entirely enveloped by a circle of leaves. Leaves equitant, coriaceous, about six or more in number, articulated to imbricating sheaths; blades elliptic-linear, acute, 1.8–3.9 cm. long, 3.5–4.5 mm. wide; sheaths conduplicate, short, 6–8 mm. long. Inflorescences one to three, springing from the upper axils, racemose, erect or arcuate, about 5.5 cm. long, apparently 9-flowered, with the short peduncle and lightly fractiflex rachis narrowly bialate. Bracts spreading, triangular-lanceolate to ovate-lanceolate, long-acuminate, amplexicaul, dorsally carinate as an extension of the bialate rachis. Flowers small, white, the lip being dark green marked with white. Perianth

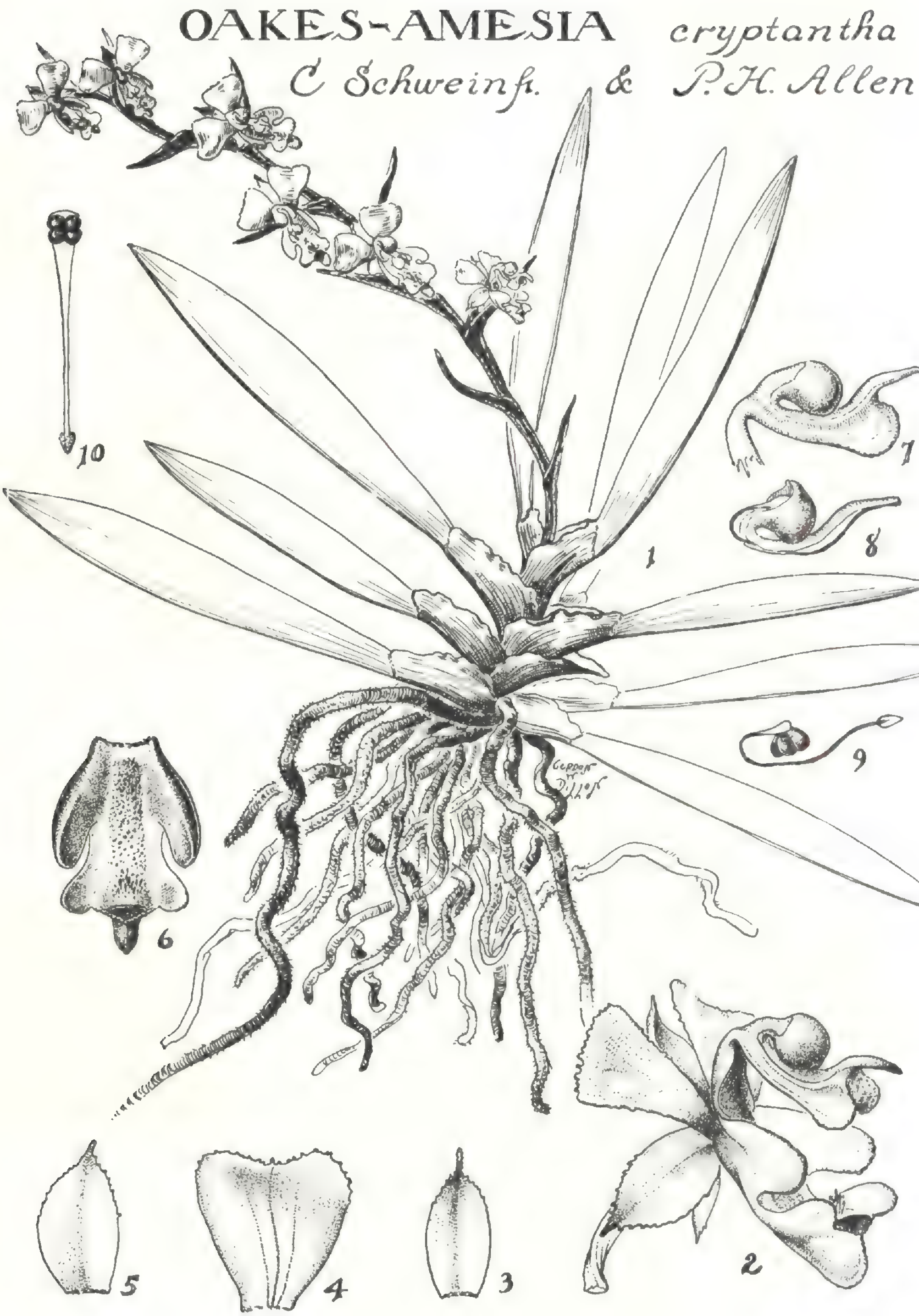
parts widely spreading. Dorsal sepal oblong-ovate, concave, mucronate, 1-nerved, dorsally lightly carinate, the upper margins being minutely erose, about 2.7 mm. long and 1.25 mm. wide when expanded. Lateral sepals obliquely ovate, concave, mucronate, 1-nerved, dorsally carinate, with the upper margins minutely erose, about 2.9 mm. long and 1.5 mm. wide when expanded. Petals triangular-cuneate, abruptly and broadly truncate to lightly retuse at the apex with the upper margins minutely erose, 3-nerved through the center, about 3 mm. long and subequally wide above. Lip complex, deeply 3-lobed in the middle, concave with the lateral lobes and the sides of the mid-lobe erect in natural position, about 3.5 mm. long, the longitudinal center traversed by a narrow tube (with opening at the apex), above which is a linear-oblong fleshy papillose band beset with hairs at the apex; lateral lobes obliquely and broadly oblong with a rounded apex, porrect; mid-lobe subquadrate-cuneate when expanded with the opening of the tube in the center of the truncate apex and with a high fleshy keel on the under surface forming a prominent mucro when viewed from above. Column short, right-angled-geniculate near the middle, about 1.5 mm. high; from the sinus of the angle in front extends a porrect elongate rostellar process about 3 mm. long which is dilated above and prominently mucronate (thus 3-lobulate), the dilated portion on each side being decurved and forming a rounded semiobovate lobule; anther imbedded on the rostellar process (i.e. incumbent), elongate, abruptly sigmoid and semiglobose-dilated above; pollinia four, small, affixed to the apex of an elongate triangular-linear stipe.

At first sight *Allen & Allen 4196* appeared to represent a typical member of the well-marked genus *Ornithocephalus*. An examination of the flowers, however, revealed characters which could not be reconciled with

EXPLANATION OF THE ILLUSTRATION

PLATE X. OAKES-AMESIA CRYPTANTHA *C. Schweinfurth & P. H. Allen.* 1, plant, twice natural size. 2, flower, from side, six and two thirds times natural size. 3, dorsal sepal, six and two thirds times natural size. 4, petal, six and two thirds times natural size. 5, lateral sepal, six and two thirds times natural size. 6, lip, from above, six and two thirds times natural size. 7, portion of column, with rostellar process and anther in place, from side, six and two thirds times natural size. 8, anther with pollinia, natural position, from side, six and two thirds times natural size. 9, pollinia with stipe and viscid disc, natural position, from side, six and two thirds times natural size. 10, pollinia with stipe and viscid disc, extended, from above, six and two thirds times natural size. *Drawn by* GORDON W. DILLON.

PLATE X



our present conception of that genus. After prolonged study, it has seemed to us the wiser course to recognize this collection as constituting a new genus.

A marked point of difference from *Ornithocephalus* is the sharply 3-lobed lip provided with a central longitudinal tube (open in front) and an overlying fleshy papillose linear-oblong band which is pubescent in front. Moreover, there is a stout trilobulate rostellar process that is very different from the slender simple attenuate rostellar process of *Ornithocephalus*. In profile the column with its rostellar process and anther suggests the head and folded legs of a praying mantis.

The name *Oakes-Amesia* was chosen to commemorate the foremost living orchidologist who has recently completed a term of fifty years as teacher, mentor and benefactor of Harvard University.

PANAMA: Prov. of Coclé, summit of Cerro Pajita, hills north of El Valle de Anton, at 1000–1200 meters altitude, epiphyte on small trees in dwarf cloud forest, January 7, 1947, *Paul H. and Dorothy O. Allen 4196* (TYPE in Herb. Ames No. 64880).

Gongora armeniaca (*Lindl.*) *Reichenbach filius* var. **bicornuta** *C. Schweinfurth & P. H. Allen var. nov.*

Herba florum colore et labelli hypochilio antice bicornuto et medio supra conspicue dentato et columnae apice utrinque angulato a specie differt.

Plant rather small, with an abbreviated rhizome. Pseudobulbs approximate, broadly ovoid, bifoliate, deeply plurisulcate, 2–3 cm. high. Leaves lanceolate-elliptic, acuminate, shortly narrowed to a subpetiolate base, plicate, with 3–5 nerves conspicuously exserted beneath, up to 12 cm. long and nearly 4 cm. wide. Scape lateral, basal, pendent, filiform below, slightly thickened above, very loosely few- (up to 5-) flowered in the upper part, about 13 cm. long: rachis of raceme lightly fractiflex,

EXPLANATION OF THE ILLUSTRATION

PLATE XI. GONGORA ARMENIACA var. BICORNUTA *C. Schweinfurth & P. H. Allen.* 1, plant, natural position, about natural size. 2, lip, natural position, from above, nearly three times natural size. 3, lip, natural position, from side, three times natural size. 4, column (with foot) and petals, natural position, about twice natural size.

Drawn by DOROTHY O. ALLEN

Plate XI

nearly 5 cm. long. Sepals pale cream-color, minutely spotted with red. Dorsal sepal erect and cucullate, obovate, acute, about 1.8 cm. long and 1.2 cm. wide above, with the mid-nerve slightly carinate without. Lateral sepals spreading-reflexed, very obliquely elliptic-ovate with the anterior margin nearly semicircular and the posterior margin nearly straight when expanded, acute, the mid-nerve distinctly carinate without, long-adnate to the column-foot at the base, about 1.9 cm. long to the posterior point of attachment and nearly 1.5 cm. wide. Petals small, dark red, very obliquely inserted on the column, sigmoid, oblong-lanceolate, with an upcurved, acute or acuminate apex. Lip very fleshy, with a broad abbreviated claw, about 1.5 cm. long in natural position, rich waxy orange with a dark red tip to the epichile; hypochile, when viewed from the side, terminating on each side in a conspicuous lightly incurved horn, with a short but prominent tooth near the middle of the upper surface, subquadrate-pandurate when viewed from above; epichile upcurved and inserted at nearly a right angle to the hypochile, triangular-lanceolate with an uncinate tip when viewed from the side, linear-triangular and sulcate when viewed from above. Column relatively short, pale cream-color dotted with red, arcuate, clavate, with a prominent angle on each side of the apex, about 1.2 cm. long, extended into a stout sulcate pubescent foot.

This concept differs rather strikingly from *Gongora armeniaca* in the color of the flowers, in the cornute anterior projections of the hypochile, in the conspicuous middle tooth on its upper surface and in the angulate apex of the column.

PANAMA: Prov. of Veraguas, region west of Santa Fé, Cerro Tute, at 1000 meters altitude, June 24, 1947, *P. H. Allen 4648* (TYPE in Herb. Ames No. 64263).

Gongora maculata *Lindley* var. **latibasis** *C. Schweinfurth & P. H. Allen var. nov.*

Herba floribus majoribus atque labelli hypochilio perlato basi triangulari nec vere cornuto a specie differt.

Vegetative portions not seen. Pseudobulbs said to be subglobose, about 5 cm. in diameter, deeply sulcate. Leaves about 30 cm. long and 10 cm. wide, grayish green. Flowers (of which I have examined two) somewhat larger than those of *Gongora maculata;* buds tawny yellow; sepals dark blood-red; petals and column green with small red spots. Dorsal sepal broadly ovate-elliptic, acute, adnate to the middle of the column, lightly concave, with revolute margins, about 2.3 cm. long and 1.3 cm. wide when expanded. Lateral sepals larger, widespreading, obliquely triangular-ovate, acuminate, with revolute margins, the base being long-adnate to the column-foot, about 3 cm. long to the posterior point of insertion and 2 cm. wide. Petals relatively small (as in the genus), long-adnate to the column, the free portion being sigmoid, linear, acute, strongly incurved in natural position. Lip very fleshy, about 2.2 cm. long, adnate to the abbreviated free apex of the column-foot; hypochile (when viewed from above) subquadrate-triangular with a very broad subbasal portion which is destitute of horns, the anterior portion in front of the broad rounded sinus produced on each side into an erect bristle; epichile narrowly triangular and acuminate when viewed from above, laterally compressed and broadly triangular with a recurved apex when viewed from the side. Column arcuate, slightly enlarged above, about 2 cm. long.

By reason of its large size, this concept appears to be quite distinct from the other members of the genus *Gongora* which have been examined. It is unusual, among the other members of its alliance, in having a lip with a very broad triangular basal portion which lacks any true horns.

PANAMA: Canal Zone, about 2 miles west of Gatun Dam, at about 184 meters altitude, April 1, 1939 (blooming time), *Butcher s.n.* (TYPE in Herb. Ames No. 64244).

Brassia Allenii *L. O. Williams ex C. Schweinfurth sp. nov.*

Herba epiphytica, robusta, sine pseudobulbo caulique. Vaginarum foliiferarum fasciculus flabelliformis. Vaginae conduplicatae, imbricatae. Folia oblanceolata vel oblongo-lanceolata vel lineari-oblanceolata, oblique acuta. Inflorescentia lateralis, axillaris, foliis brevior, laxe pauciflora. Flores pro genere parvi. Sepala similia, lineari-lanceolata, supra longe attenuata. Petala quam sepala breviora et latiora, oblique et anguste lanceolata, longe attenuata. Labellum ovatum vel suborbiculari-ovatum, antice abrupte in apicem anguste triangularem productum; discus callis duobus brevibus carnosis apice in dentem productis ornatus. Columna abbreviata, crassa.

Plant epiphytic, more or less robust. Roots fibrous, glabrous, stout, numerous. Stems or pseudobulbs lacking, their place being taken by a flabellate cluster of leaf-bearing sheaths. Leaf-sheaths several to numerous, imbricating, conduplicate, nervose, surrounded on each side by abbreviated often non-leaf-bearing sheaths. Leaves oblanceolate to oblong-lanceolate or linear-oblanceolate, very obliquely acute with one side of the apex much surpassing the other, gradually narrowed to a complicate or conduplicate base, plicate, many-nerved with about seven to nine nerves prominently exserted beneath, commonly about 18.5–30 cm. long and 2.3–2.7 (rarely 3.8) cm. wide. Inflorescence in the axil of an upper leaf-sheath, loosely 6- to 7-flowered from near the base, distinctly shorter than the leaves, gently recurved. Floral bracts conspicuous, deeply concave, ovate, amplexicaul, acute or acuminate, scarious, many-nerved, slightly sur-

EXPLANATION OF THE ILLUSTRATION

PLATE XII. BRASSIA ALLENII *L. O. Wms. ex C. Schweinfurth.* 1, plant, natural position, about one half natural size. 2, flower, from front, about five sevenths natural size. 3, column and base of lip, from side, about twice natural size.

Drawn by DOROTHY O. ALLEN

Plate XII

passing the pedicellate ovary, the lower ones 1.9–2.7 cm. long. Flowers rather small for the genus, non-resupinate in natural position (i.e. with the lip uppermost). Dorsal sepal linear-lanceolate, long-attenuate with conduplicate upper portion, about 3.7 cm. long and 5 mm. wide below. Lateral sepals similar but apparently a little longer and narrower (sometimes slightly broader), about 4.3 cm. long and 4 mm. wide. Petals obliquely and narrowly lanceolate, long-attenuate above with conduplicate margins, about 3.3 cm. long and 6 mm. wide below. Lip ovate or suborbicular-ovate, with the lobulate anterior margins terminating abruptly in a more or less elongate triangular or linear-triangular mucro, subcordate at base, about 1.5–2.1 cm. long and 1.2–1.5 cm. wide near the base; disc at the base just in front of the column with a pair of short approximate fleshy keels which are deeply constricted in front forming a pair of conical complanate teeth. Column very short and stout, wingless, about 3 mm. high at the back.

This species is extremely variable both vegetatively and florally. The measurements of the most complete specimen, which has been taken as the type, are uniformly somewhat smaller than those of other collections. *Brassia Allenii* seems to be related to the Venezuelan *Brassia glumacea* Lindl., but differs in having a much stouter habit, in having the racemes markedly shorter than the leaves and in its apparently dissimilar lip.

This concept was first considered as new and was named by Dr. Louis O. Williams, but has remained undescribed until this time.

PANAMA: Prov. of Panama, summit of Cerro Campana near Campana, at about 1000 meters altitude, in cloud forest, October 2, 1947, *Paul H. Allen 5150* (TYPE in Herb. Ames No. 64857); Prov. of Coclé, vicinity of El Valle, at 800–1000 meters altitude, sepals and petals dark reddish brown, lip yellow, fragrant, August 17, 1937, *P. H. Allen*

374; Prov. of Coclé, mountains beyond La Pintada, at 400–600 meters altitude, February 17, 1935, *A. A. Hunter & P. H. Allen 592* (old fruit); Prov. of Coclé, region north of El Valle de Anton, vicinity of La Mesa, at about 1000 meters altitude, very common in dark wet forest of higher elevations, November 12, 1941, *P. H. Allen 2830;* same locality, Finca Muñoz, at 800–1000 meters altitude, Feb. 2, 1942, *P. H. Allen 2922;* same locality, at about 700–800 meters altitude (flowered by Mr. Elmer Ohlson, September 10, 1942), *P. H. Allen 2963;* Prov. of Coclé, "Loma del Tigre," hills north of El Valle de Anton, at 1000 meters altitude, November 16, 1946, *P. H. Allen 3804.*

Lockhartia amoena *Endres & Reichb.f.* var. **triangulabia** (*A. & S.*) *C. Schweinfurth & P. H. Allen comb. nov.*

Lockhartia triangulabia A. & S. Sched. Orch. 8 (1925) 80.

In view of the great variability shown by the lip in the numerous collections of *Lockhartia amoena*, it appears to us that the concept described as *Lockhartia triangulabia* represents only an extreme form of the earlier species. We therefore propose the above combination.

In conformity with our present view of regarding the concept *Ornithidium* Salisb. as being referable to the large and polymorphic genus *Maxillaria* Ruiz & Pav., the two following transfers become necessary.

Maxillaria Jenischiana (*Reichb.f.*) *C. Schweinfurth comb. nov.*

Ornithidium Jenischianum Reichenbach filius in Bonpl. 2 (1854) 18.

Maxillaria sanguinolenta (*Lindl.*) *C. Schweinfurth comb. nov.*

Ornithidium sanguinolentum Lindley Orch. Linden. (1846) 22, no. 117.

Ornithocephalus polyodon *Reichenbach filius* in Linnaea 41 (1876) 33.

Since this species, originally found in Ecuador, was described from two inflorescences only, it seems wise to append a more detailed description as afforded by a recent Peruvian collection consisting of three complete plants.

Plant rather large and stout for the genus, epiphytic, about 11–19 cm. tall. Stems abbreviated as in the genus, entirely concealed by a circle of nine to eleven crowded imbricating sheaths of the leaves. Leaf-sheaths conduplicate with a scarious band on the upper margin. Leaves elliptic-lanceolate to linear-lanceolate, more or less acuminate, usually lightly oblique above, somewhat narrowed to an obliquely articulated base, about 3 (outer blade) –16 cm. long, 0.85–1.4 cm. wide. Scapes lateral in the axils of leaf-sheaths, usually two to each plant, suberect or flexuous to arcuate, about 9.5–19.5 cm. long, entirely glandular-setulose (slightly so below), racemose above; peduncle short, 4 cm. or more long, with three or more remote, spreading, semiamplexicaul sheaths; raceme up to 14.5 cm. long, loose or subdense, several- (8) to many-flowered. Floral bracts spreading, suborbicular-ovate, semiamplexicaul, glandular-ciliolate. Flowers rather large for the genus, with membranaceous wide-spreading segments. Dorsal sepal deeply concave, suborbicular-obovate, broadly rounded at the apex, irregularly glandular-ciliate (especially on the lateral margins), rather densely glandular-setose on the outer surface, 1-nerved, about 6 mm. long and 4 mm. wide. Lateral sepals oblong-obovate, broadly rounded above, lightly concave, somewhat oblique, sparingly serrate, rather densely glandular-setose without, 1-nerved and dorsally keeled,

about 5.5 mm. long and 3.8 mm. or less wide. Petals cuneate-flabellate with recurved sides in natural position, oblong-obovate when expanded, broadly rounded at the apex, 1-nerved, about 5 mm. long, 3.5–4.2 mm. wide, 2- to 3-nerved. Lip deeply 3-lobed, shorter than the other segments in natural position, with saccate base, erect lateral lobes and recurved mid-lobe, when expanded about 6.5 mm. long and slightly wider across the base; lateral lobes small, divaricate, triangular-oblong, with a recurved convex apex; mid-lobe much larger, subquadrate-ovate when expanded, slightly dilated above and below, rather abruptly narrowed above to an acute tip, 7-nerved; disc with a transverse subelliptical pluridentate callus which extends as a toothed ridge from the base of the lateral lobes, continues in a curved line in front of the lateral lobes and is extended across the base of the mid-lobe. Column very small, clavate, with a reflexed linear rostellum.

In the Ames Herbarium there is a drawing of *Ornithocephalus polyodon* from the Reichenbach Herbarium consisting of two flowering racemes and a rather detailed floral analysis. The latter shows a close agreement with the flowers of the Peruvian collection, having similar oblong-obovate sepals with a broadly rounded apex. The petals are shown as sometimes broadly rounded and sometimes (as described) retuse at the apex. The lateral lobes of the lip (as drawn) appear to be subequal in size to the mid-lobe. The type description, as well as the Reichenbach drawing, shows that there is a toothed upper margin of the petals, a character which does not appear in our specimen.

Ecuador: (Type).

Peru: Loreto, Río Mazán, at 100–125 meters altitude, February 1935, *José M. Schunke 391*.

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JANUARY 17, 1949 VOL. 13, NO. 7

MAIZE GRANARIES IN MEXICO

BY

EFRAIM HERNANDEZ XOLOCOTZI [1]

I. INTRODUCTION

THIS study attempts to follow the development of the maize granary, an important element of material culture, in Mexico where maize has been and still is the basic source of food. Sufficient information is now available to permit the presentation of a tentative outline of this development from the pre-Conquest period to the present day. Further anthropological and ethnobotanical studies along these lines may result eventually in the establishment of significant correlations between granary types and indigenous cultures. Such correlations would be of great value to scientists engaged in plant exploration, in connection with maize research of either a practical or a theoretical aspect, since Indian cultures have acted in part as isolating mechanisms resulting in the production and maintenance of maize ecotypes.

In the Western Hemisphere, maize was the cereal which served as the economic basis for civilization. Archaeological studies have brought to light various cultures with an incipient agriculture based on plants other than maize (Zingg 1939 and Anderson 1947); however, it was not until after the domestication and spread of

[1] Rockefeller Foundation Fellow from Mexican Agricultural Program and Agrónomo "B" de la Secretaria de Agricultura y Ganaderia, Mexico.

maize that the South and Middle American civilizations were able to flourish. The widespread adaptation of maize agriculture resulted in a vital interdependence between this domesticated cereal and man. After domestication, maize could no longer subsist without the aid of man, and man himself relied more and more upon the product of this crop as his main source of food. This dependence on maize is still an outstanding characteristic of most of the Latin American countries today and of the Indian populations in particular.

It is probable that the problem of maize storage arose with the beginning of maize agriculture. With an increase in population resulting from an initial food surplus, maize storage took on an even greater importance. As the culture increased in complexity, this problem took on a group as well as an individual significance. By the time of the Conquest of Mexico, attention was devoted to the maize granaries by the rulers and priests, by the rich and the poor, by the craftsmen and the peasants. The tribal and family granaries represented a savings account which kept away disaster and maintained social vigor. Failure of the family granary meant slavery; failure of the tribal granaries meant social disintegration.

However, in spite of extensive cultural similarities among the Indian populations of Mexico, the development of the storage structures have followed various lines. Diversification in granary types resulted from: a) differences in climate, b) differences in materials available for construction, c) special cultural traits of the society, and d) variations in the cultural level.

II. The Problem of Maize Storage

Maize became a dominant crop in the agricultural economy of the American civilizations because it possessed the favorable characteristics generally found among

the cereals. These are as follows: 1) the seed is a highly nutritive caryopsis, 2) the production of seed is highly efficient, 3) the seed can be handled and stored with ease, 4) the maize plant lends itself to the use of simple methods of cultivation, and 5) the plant has a wide tolerance to many and varied ecological conditions.

The nature of the seed favored its storage. However, the storage of the maize crop required special attention due to the following reasons: 1) several pests and diseases attack the grain, 2) a surplus stock would prevent the calamities of a poor crop, and 3) climatic variations often resulted in considerable decreases in yield.

No doubt the chief interest of the people was the production of an essential minimum amount of grain each year. This is suggested by the complex religious pattern centered around the maize theme, the interest in astronomy and its relation to the cultivation of maize, and the use of mixed seed of maize lines adapted to various climatic conditions. Once the crop had been obtained, it was necessary to protect it until the following harvest since this was periodical. In addition, the demands of a non-agricultural population, and the use of marginal and sub-marginal lands for agriculture due to population pressure, all stimulated the development of some method of storage.

Thus it is seen that the problem of storage was concomitant with the cultivation of maize. The method of storage could vary, but under any condition it necessitated the development of a special cultural pattern. The term maize granary is here used to designate the material element designed for the solution of this problem.

III. Archaeological Period
(circa 500–1100 A.D.)

Anthropological studies show that the Mexican Indian

cultures developed intricate religious patterns at an early stage. With an increase in populations and the flourishing of these societies, this tendency led to the establishment of a strong theocracy, later aided by rulers in charge of the secular functions of the group. Under these conditions, the cultures followed a dichotomous development; on the one hand, of the ruling classes and their magnificent material culture, and on the other hand, of the ruled masses with a less spectacular but more stable form of material culture which has persisted to date in many areas of Mexico.

It was not until recently that archaeologists began to pay attention to the cultural patterns of this larger part of the Indian population. The increased interest in pottery types indicates a tendency toward the study of this rich source of information. As it is, the recorded information on maize granaries from archaeological remains is extremely meager. The perusal of the extensive literature dealing with the impressive ruins in the Mayan area, San Juan Teotihuacan, Monte Alban, Mitla and La Venta, all undoubtedly of great religious importance, adds very little to an understanding of our particular problem.

S. Linné (1934) describes what are probably the oldest remains definitely related to maize storage. He writes of the results of his excavations of some of the smaller out-lying ruins of the ancient religious center at San Juan Teotihuacan, State of Mexico:

> "While purely utilitarian pottery was almost entirely absent among the finds that were made below the floors of the ruin, it appears that almost all the vessels just described have served some practical purpose or other, e.g. for serving up food. There are also numerous fragments of storage vessels. These were generally of ovoidal shape, with a relatively narrow mouth, and from many of the fragments it is evident that the vessels often were of considerable size."

As will be seen later, this method of storage was used

by the farmers of Mexico City at the time of the Conquest (Pl. XVI, A).

Archaeological studies in the Tarahumara region of northwestern Mexico, in the States of Sonora and Chihuahua, give a more complete picture of the methods used in storing maize. According to the works of C. Lumholtz (1902) and R. M. Zingg (1940), these are as follows: 1) underground cavities, 2) niches of caves walled in, 3) rectangular and cylindrical stone and mortar structures, 4) wattle and clay daub containers, and 5) vasiform structures made of coiled grass and clay daub.

In 1931, Robert M. Zingg carried out extensive studies in the Rio Fuerte region of southern Chihuahua. From the material obtained, he concluded (1940) that it represented a Basket-Maker and a Cave-Dweller cultural phase of the ancient Tarahumaras. The methods of maize storage used during the Cave-Dweller phase are those included above under numbers one to three. These are of special interest because they are still followed in part by the modern Tarahumaras, and they are not reported from any other group in Mexico.

During the Basket-Maker phase, Zingg finds "large bowl-like containers, 24″ in diameter and 8″ deep" having a funerary context but probably related also to an element used in the storage of maize. These containers "made by coiling rolls of grass imbedded in mud as binder" appear to Zingg as "a simplification of the coiled mud and grass storage structures of the Cliff Houses of the Casas Grandes archaeological phase of northern Chihuahua" described by Lumholtz (1902). These latter storage structures were found by Lumholtz at Cave Valley, close to Pacheco, and at Aros River, south of Chuicuichupa, both localities in the State of Chihuahua within the Tarahumara region (Pl. XIII, A, B). Lumholtz showed them to be maize granaries which he related to

the vasiform granaries (*cuezcomatls*) found in use in 1902 in the central Mexican States of Tlaxcala and Veracruz. As this type of storage structure is used at the present time in Tlaxcala and Morelos, it seems that an uninterrupted sequence is present in the use of this type of granary from the archaeological to the present period.

Because of the relationship of these forms of granaries, it is of interest to include the description of the structures (Plate XIII) discovered by Lumholtz (1902):

"The most unique feature of this cave, however, is the cupola-shaped structure which stands in an open space in front of the house group, near the mouth of the cave, but still under its roof. Its height, measured inside, is twelve feet, and its widest inside diameter is eleven feet. Its walls average eight inches in thickness. It has one aperture three feet wide at the top, another one of the same diameter near the base, and there are several others nearly opposite each other. In the two upper ones are seen distinct impressions of timber in the plaster.

"The building was made by twisting long grass into a compact cable and laying it up one round upon another. As the coil proceeded, thick coats of plaster were laid on inside and outside. This plaster, which is the same material as that of which the houses are constructed, got thoroughly mixed with the straw during the process of building, and the entire structure was finished without any opening except the one at the top. The other apertures were undoubtedly cut out afterward. There is no trace of withes or other binding material to hold the straw cables in place. They are kept in position only by the plaster, which here, as in the houses, is almost as hard as the conglomerate of the surrounding rocks."

Further on he adds:

"Two of them were deeply sunken into the floor of the cave, and inside of them we found between the rubbish and debris that filled them, several grains of corn and some beans."

A study of the findings of Isabel Kelly (1947) at Apatzingan, Michoacan, along the Pacific coast of Mexico, suggests the presence of remains which may be the foundations of granaries similar to those now in use along the coast of Guerrero. However, a sufficient knowledge is lacking for accurate determination.

SUMMARY—ARCHAEOLOGICAL PERIOD (500–1100 A.D.)

Granary Type	*Indian Group*	*Distribution*
1. Subterranean	Tarahumara	Sonora and Chihuahua
2. Niches of caves	Tarahumara	Son. and Chih.
3. Rectangular and cylindrical, stone and mortar	Tarahumara	Son. and Chih.
4. Wattle and clay daub	Tarahumara	Son. and Chih.
5. Vasiform, coiled grass and clay daub	Tarahumara	Son. and Chih.
6. Clay jars	Teotihuacan	San Juan Teotihuacan, Mex.

IV. Pre-Conquest Period (1100–1518 A.D.)

For a knowledge of the cultures found in Mexico at the time of the Conquest, two extensive sources of information are available: a) the Codicis, and b) the writings of men who lived in Mexico during the few decades following the Conquest. It seems reasonable to assume that these historical documents refer to cultural traits of a well-established pattern which remained unchanged for some time after the Conquest. For this reason, this information is interpreted as a reflection of conditions existing previous to the Conquest.

The Codicis are a form of pictorial writing used by the Mexican tribes to record such information as tribal history, rights to land ownership, commercial transactions and tribute lists. The pictorial technique varied widely probably as the result of a constant development from pure pictorial representation to a semi-phonetic writing. Of the Codicis which escaped destruction, the most important ones to our problem are the Codex Mendoza, the Historia Chichimeca, the Yanhuitlan Codex, the Codex Troano-Cortesiano and the Lienzo de Tlaxcala.

The information gleaned from these sources may be divided into two categories: a) one referring to the storage structures used by the rulers, and b) the other re-

ferring to the maize granaries of the farmers and craftsmen. In most cases the same type of granary was used by both classes, but the small family granary types are the ones that have survived and give a distinctive appearance to many of the Indian communities of present-day Mexico.

A. Imperial Granaries

Bernal Diaz del Castillo (1568) gives an insight into the organization of the palace of Moctezuma when he states:

> "Dejemos de hablar de la costa y comida de su casa, y digamos de los mayordomos y tesoreros y despensas y botelleria y de los que tenian cargo de las casas adonde tenian el maiz."

Thus we learn that Moctezuma had overseers and "treasurers" who were in charge of the ruler's pantries, "wine" rooms and houses where maize was stored.

Fr. Bernardino de Sahagun (1529–1590) amplifies this information in his section dealing with the warehouses of the Aztec ruler wherein he writes:

> "Otra sala del palacio se llamaba petlacalco. En este lugar posaba un mayordomo del señor, que tenia cargo y cuenta de todas las trojes de los mantenimientos de maiz que se guardaba para proveimiento de la ciudad y republica, que cabian a cada dos mil fanegas de maiz, en las cuales habia maiz de veinte años sin dañarse; tambien habia otras trojes en que se guardaba mucha cantidad de frijoles."

In addition there were other warehouses (*trojes*) for salt, peppers and two kinds of pumpkin seeds.

As much of the imperial supplies was obtained as tribute exacted from the towns under the Aztec domination, the Codex Mendoza (Kingsborough 1831–1848, Long 1942) is an important source of information. This Codex was made by order of Don Antonio de Mendoza, Viceroy of Nueva España from 1535 to 1550, and was intended for King Charles V. It was painted by Mexican

artists and the pictorial technique shows no Spanish influence. It is believed to be a copy of an older Codex made in 1511 to record Moctezuma's tribute list. Throughout this document, the measure of the tribute to be paid in terms of maize, beans, chia (*Salvia hispanica*) and quautli (*Amaranthus caudatus*), is indicated as a large wooden granary of the log-cabin type.

Other authors writing at a much later period suggest that the following two types of granaries were also used by the Aztec rulers: large cask-like containers made of wattle and clay daub and kept within the rooms of the palace (Torquemada 1723); and *cuezcomatls* (vasiform granaries) according to Fray Alonso de la Mota y Escobar (Simpson 1934).

The following four types of imperial granaries may therefore be recognized:

1. Rooms within the palace. This type of storage is described by Diaz del Castillo (1568) and Sahagun (1529–1590).

2. Log-cabin granary (Pl. XIV, A). In 18 of the plates of the Codex Mendoza (Kingsborough 1831–1848) a total of forty of these figures are illustrated, and in all cases the Spanish text refers to them as "troxes." All are strikingly similar and seem to represent a cubical structure consisting of low corner posts, a plank floor, log or board walls interrupted at about the middle by a circle, and a plank roof. The representations of various types of grains are drawn above the figures of these structures, and it is evident, from the rest of the information given, that these granaries were used as measures of the yearly tribute which had to be given to the Aztec ruler. There is no indication regarding the manner in which the walls were held together at the corners, and

it seems best to regard this lack of detail as a simplification leading to economy of effort on the part of the artist. The color and position of the circle on the front wall suggest a small wooden door similar to the one found in log-cabin structures common among the Mixtec Indians today.

Anderson and Barlow (1943) made a special study of these figures, and their findings may be summarized as follows: the figures represent large wooden granaries with a capacity of four or five thousand "fanegas" (about 10,000 bushels); these "troxes" were used as units of measure of the yearly tribute required of the various provinces in terms of maize, beans, chia and quautli; these granaries were built at strategic localities throughout the Valley of Mexico and into Oaxaca as far as Oaxaca City.

Finally, at a late date Francisco Saverio Clavijero (1780) gives a full description of this type of granary and his description is included since it has been repeated by Prescott (1843), Brasseur de Bourbourg (1858) and Bancroft (1875).

"Eras, y Graneros. Tanian eras para deshojar, y desgranar las mazorcas, y graneros para guardar el grano. Estos eran cuadrados, y por lo comun, de madera. Servianse para esto del *ojametl*, arbol altisimo, de pocas ramas, y estas mui delgadas, de corteza tenue, y lisa, y de contestura flexible, pero dificil de romperse, y rajarse. Formaban el granero, disponiendo en cuadro, unos sobre otros, los troncos redondos e iguales de ojametl, sin otra trabazon que una especie de horquilla en su estremidad, para ajustarlos, y unirlos tan perfectamente, que no dejasen paso a la luz. Cuando llegaban a cierta altura, los cubrian con otra trabazon de pinos, y sobre ella construian el techo, para defender el grano de la lluvia. Estos graneros no tenian otra salida que dos solas ventanas, una pequeña en la parte inferior, y otra grande en la superior. Los habia tan espaciosos que podian contener cinco mil, seis mil, y aun mas fanegas de maiz."

He goes on to say that some of these structures were

still to be found in places at some distance from the capital (Mexico City) and that they seemed old enough to have been constructed before the Conquest.

3. *Cuezcomatls*, vasiform grass and daub granaries. In 1609, Fray Alonso de la Mota y Escobar (Simpson 1934) includes the following statement in his memoirs with reference to San Juan Cuezcomatepec, a village 25 kilometers northwest of Cordoba, Veracruz:

> "Hablase en este pueblo lengua mexicana perfecta llamase en ella *Cuezcomatepec* que suena el pueblo de los troxes porque dizen las tenia aqui *Motezuma* de mucha cantidad de mahiz que por ser tan frio y seco se conseruaua aqui como en deposito para los tiempos de sus hambres."

As will be shown later it seems reasonable to assume that the Indian word *cuezcomatl* refers to the vasiform type of granary.

Most students of the Nahuatl language indicate that the etymology of the word *cuezcomatl* is not known. From a very ancient period the word has meant a granary and *cuezcomatl* has been used as a root word in the composition of other words. However, Siméon (1885) writes in his Dictionnaire de la Langue Nahuatl:

> "Cuezcomatl, s. Havre-sac, magasin de pain; sommet de la tête, crâne. En comp. *nocuezcon*, mon crâne; *tocuezcon*, notre crâne, le crâne en general. Avec les postp. *c*, *tlan: cuezcomac*, dans le havre-sac, dans le grenier; *cuezcomatitlan*, parmi les havre-sacs."

While Garcia Cubas (1888–1891) adds that *comatl* means *vasija* or container. It seems then that *cuezcomatl* might mean a container in the form of a skull. A study of Pl. XIII, the vasiform grass and daub granary of the ancient Tarahumaras related to the present-day granaries, suggests the possible reason for the use of this word for these structures.

4. Wattle and daub cask-like granaries. Torquemada (1723) has a chapter in which he relates the looting of

"Moctecuhcuma's" warehouses by the Indian allies of Cortes and by Pedro de Alvarado. Of the containers in which the royal supplies were kept, he says:

"Estaba el Cacao en unas Vasijas hechas de Mimbres, tan grandes como Cubas, que seis Hombres no las podian abarcar; estaban embarradas por de dentro, y por de fuera, y asentadas por orden, como Cubas; servian de Troxes para el Maiz, y otras Semillas, y se conservaban bien en ellas. . . ."

B. Family Maize Granaries

The information recorded about the family maize granaries of this period presents for the first time the extreme diversity which is to be expected in this country of numerous Indian cultures.

a. Permanent and semi-permanent family granary types

1. Niches of caves. The use of this method of maize storage is not reported for this period, but undoubtedly it was in use among the Tarahumara Indians since it has been found among them during the Archaeological Period and the 19th Century.

2. Rectangular and cylindrical stone and mortar structures. The same may be said for this type of granary as has been said for the previous type.

3. Wattle and clay daub. Probably in use among the Tarahumara, as a similar reasoning holds for this type as for Type 1.

4. *Cuezcomatl*, vasiform grass and daub granary (Pl. XIV, B, C, D). Several of the town names included in the Codex Mendoza (Kingsborough 1831–1848) and the Historia Chichimeca (Boban 1891) are combinations utilizing the Indian word *cuezcomatl*. As this is the

name used at present for the vasiform granaries in the States of Tlaxcala and Morelos, a special study was made of the town glyphs in the Codicis. Those for Cuezcomatlyyacac (Cuezcomatl iyacac), Cuezcomayxtlahuacan, Cuezcomahuacan and Cuezcomatitlan all consist of a dominant vasiform figure with the following characteristics: a) the structure seems to rest on a rectangular foundation built on top of roundish stone corner supports, b) the vasiform figure is divided by several horizontal lines suggesting a structure made of several sections, and c) the top of the structure is shown as an open circular mouth except in Cuezcomatlyyacac in which a sort of round lid is indicated.

Wherever interpretations of the town glyphs are made, *cuezcomatl* is translated as *troxe*, *granero* or granary. For instance, Clark (1938) gives the following meanings in his analysis of the Codex Mendoza:

Cuezcomahuacan: place of granaries
Cuezcomayxtlahuacan: place of the plain of bins
Cuezcomatitlan: amongst the granaries
Cuezcomatliyacac: in the beginning of the granaries

It seems then that the farmers of the Mexican central plateau at the pre-Conquest period were using a vasiform maize granary which is related to the archaeological remains of the Tarahumara and to the present day *cuezcomatls* of Tlaxcala and Morelos.

Sahagun (1529–1590) suggests the use of this type of granary when he writes:

"De algunos zazamiles de los muchachos que usa esta gente mexicana, que son los 'que cosa y cosa de nuestra lengua' (Acertijos).? Que cosa y cosa una vieja que tiene los cabellos de heno, y esta cerca de la puerta de casa? Es la troje de maiz."

Torquemada (1723) also seems to refer to this type of granary when, in speaking of the custom of punishing

those who stole maize from the granaries, he states that these "troxes" are like very large vessels (*tinajas*) with their mouths on the uppermost part and anyone wishing to take out the contents must climb into it. The Lienzo de Tlaxcala (Anonymous 1892) includes two perfect representations of these granaries.

5. Clay jars (Pl. XVI, A). This figure reproduced from the illustrations which form part of the work of Sahagun (1529–1590) depicts the cycle of activities of the good farmer. The storage of the harvest in large clay jars is clearly shown.

In the northwestern part of Mexico, among the Cahita-speaking Indians, today represented by the modern Yaqui and Mayo of southern Sonora and northern Sinaloa, Beals (1943) has found that during the pre-Conquest period maize sometimes "was cached underground in pottery vessels stoppered with clay."

6. Log-cabin type of granary. Plate XVI, B, reproduced from Sahagun (1529–1590), shows the storage of the maize harvest by a Mexican family. The granary consists of stone corner posts, a base made of boards or planks, and walls of logs or boards placed horizontally. Economy of detail on the part of the artist may account for the lack of detail as to the method in which the corners were formed. Two stones shown at the upper corners of the structure probably refer to rocks used to hold down the thin board or wooden shingle roof. The dimensions of the front wall as shown must be about 5 by 8 feet.

In spite of the marked differences already noted between the rulers and the lower economic classes in the Mexican Indian cultures, it seems reasonable to assume that the richer agricultural families tended to use the same type of granaries as utilized by the tribal rulers. For

this reason, the use of the wooden log-cabin type of granary by the family group is also confirmed by the information given in the Codex Mendoza (Kingsborough 1831–1848) and the Yanhuitlan Codex (Jimenez Moreno and Mateos Higuera 1940) which will be discussed later.

7. *Cincalli*, highland crib. A characteristic crib-like wooden granary known as *cincalote* is used today in a limited area to the south of Mexico City (Pl. XVIII, A). Sahagun (1529–1590) seems to refer to this type of granary when, in describing the feasts and ceremonies observed by the lapidaries, he states:

"Al otro que se llamaba Cinteotl tambien le componian como a varon, con una caratula labrada como mosaico, ... y ponianale en un tablado alto de donde estaba mirando, el cual se llamaba cincalli, compuesto de cañas de maiz a manera de jacal; . . . ."

b. Temporary methods of maize storage

1. Rafters. Sahagun (1529–1590), describing the habits and labors of the Mexican farmer born under the favorable sign Ce Tochtli, says that he was diligent, hard-working, careful of his crops and:

"asi abundantemente cogia de todas maneras de legumbres y henchia su casa de todas maneras de maiz, y colgaba por todos los maderos de su casa sarteles de maiz. . . . "

2. *Tapanco*, loft and interior of the house. This method of storage is reported to have been in use among the Cahita Indians (Beals 1943) who inhabited the dry semi-tropical coastal plains of Sonora and Sinaloa.

3. *Enramada*. Beals (1943) finds that the Cahita Indians also stored maize on the cob on *enramadas* which are raised platforms built as separate structures or as annexes to the front of the native houses (Pl. XXI, C, D).

With regard to the Mayan groups, the methods of maize storage during this period are unknown. The Codex Troano-Cortesiano suggests the use of clay jars, but no definite information is available.

SUMMARY—PRE-CONQUEST PERIOD (1100–1518 A.D.)

Granary Type	*Indian Group*	*Distribution*
A. Imperial Granaries		
1. Rooms within palace	Aztec	Valley of Mex.
2. Log-cabin granary	Aztec	Valley of Mex.
	Mixtec	Mixteca of Oax.
3. *Cuezcomatl*, vasiform, grass-daub	Aztec	Valley of Mex.
	Mazapan	Puebla
	Tlaxcalan	Tlaxcala
4. Cask-like, wattle-daub	Aztec	Valley of Mex.
B. Family Granaries		
a. Permanent and semi-permanent structures		
1. Niches of caves	Tarahumara	Son. and Chih.
2. Rectangular and cylindrical, stone and mortar	Tarahumara	Son. and Chih.
3. Wattle and clay daub	Tarahumara	Son. and Chih.
4. *Cuezcomatl*, vasiform, grass-daub	Tarahumara	Chihuahua
	Aztec	Valley of Mex.
	Mazapan	Puebla
	Tlaxcalan	Tlaxcala
5. Clay jars	Aztec	Valley of Mex.
	Cahita	Son. and Sinaloa
	Mayan (?)	Yucatan (?)
6. Log-cabin	Aztec	Valley of Mex.
	Mixtec	Mixteca of Oax.
7. *Cincalli*, highland crib	Aztec	Valley of Mex.
b. Temporary methods of storage		
1. Rafters	Aztec	Valley of Mex.
2. *Tapanco*, loft and interior of house	Cahita	Son. and Sin.
3. *Enramada*	Cahita	Son. and Sin.

V. Immediate Post-Conquest Period (1520–1600 A.D.)

Fundamentally the main social change which took place from the pre-Conquest to the Conquest periods consisted of a substitution of a Spanish theocratic-colonial government for the native theocratic-tribal ruler organization. As far as the Indian population was concerned, one master was substituted for another. The established rhythm of activities continued almost unaltered, in spite of the localized demands for Indian labor to work the mines. Various crops were introduced at this time, but maize continued to be the main source of food, and undoubtedly the methods of maize storage of the preceding period were also in use at this time by the family groups.

The establishment of the Encomienda system of land holdings placed the favored Encomendado in the position of exacting tribute from the Indian groups under his control. With regard to the storage of maize under the Encomienda, the Yanhuitlan Codex contains some valuable information. This Codex has been described in detail by Jimenez Moreno and Mateos Higuera (1940), and Anderson and Finan (1945) have added some pertinent data. It shows a large log-cabin type of structure used as a measure for the amount of maize which the people of Yanhuitlan, Oaxaca, were obliged to produce for the Encomendado Don Domingo in order to satisfy what was prescribed in the required valuation made by the Viceroy Don Antonio de Mendoza on October 26, 1548. This structure is very similar to the wooden log-cabin type of granary still in use in this region of the Mixtec Indians (Pl. XVII, D).

SUMMARY—IMMEDIATE POST-CONQUEST PERIOD (1520–1600 A.D.)

In spite of the Conquest, the agricultural Indian population of Mex-

ico continued to use the same types öf maize granaries as those existing before the Conquest. The granary system of the Indian rulers came to an end shortly after the Conquest, but the new Encomienda system began using some of the same methods of maize storage. The only definite information in this regard is that given for the use of the wooden log-cabin type of granary used in the Encomienda of Yanhuitlan, Oaxaca, among the Mixtec Indians.

VI. Late 19th Century Period

With regard to the study of maize granaries, the only important change after the political independence of Mexico was the substitution of the Hacienda system for the Encomienda. In general, the Indian population continued to use its characteristic methods of maize storage. However, the prolonged absence of a definite tribal organization and the increase in the non-Indian population resulted in a gradual mixing of granary types, a degeneration in building techniques, the introduction of foreign elements, and the disappearance of Indian granary types over large areas of Mexico.

A. Hacienda Granaries

Very little information is available as to the methods of maize storage under the Hacienda system. It is to be expected, however, that these would show a strong foreign influence.

1. Conical stone and mortar structures. These remarkable granaries, recently photographed by P. C. Mangelsdorf (Pl. XIX, A, B), are found in a small area in the States of Aguascalientes, Zacatecas and Jalisco (I. Kelly, in correspondence). These conical structures have walls of adobe faced with lime mortar and small stones. They have a winding stairway on their outer surface leading to an inlet close to the apex. A large rectangular door at the base serves for the removal of the

grain. Their conical shape gives them a high mechanical efficiency for the storage of grain. It is estimated that the larger structures have a capacity of about eighty metric tons. Their relationship to indigenous or foreign structures is unknown.

2. Cubical stone and mortar warehouses. L. Hernandez Xolocotzi (in correspondence) reports that during this period, the Haciendas of Tlaxcala used warehouses which consisted of masonry walls one meter in thickness forming large rectangular rooms 20 meters in length and 8 by 8 meters on the side, with ventilating holes close to the roof.

B. Family Maize Granaries

Three men in particular have published extensive and comprehensive descriptions of the maize granaries in Mexico in their reports of archaeological expeditions during the final years of the 19th Century: A. F. Bandelier (1884), C. Lumholtz (1902) and F. Starr (1894, 1899, 1899–1900, 1901–1903, 1908).

a. Permanent and semi-permanent structures

1. Niches of caves. Lumholtz (1902) reports this method of maize storage among the Tarahumara Indians at Yepochic, Chihuahua.

2. Rectangular and cylindrical stone and mortar structures. This type of granary was used among the Tarahumara of Sonora and Chihuahua, and the Huicholes of Nayarit (Lumholtz 1902). Of the Huicholes at Batista, Nayarit, Lumholtz writes:

"The corn when shelled is kept in round store-houses made of stone and mud. It is put in from above, and taken out through an opening near the ground, a stone serving as a door for this aperture, which is

kept tightly closed. The store-houses are very small, as the Huicholes harvest only from four to five fanegas of corn a year."[1]

3. *Cuezcomatl*, vasiform grass-daub structure. This type of granary (Pl. XV, A), previously described from the Tarahumara area and the Mexican central plateau, seems to be confined during this period to the States of Tlaxcala, Puebla and Veracruz (?). Its apparent absence from Morelos is probably due to lack of information.

Lumholtz (1902) compares the archaeological remains of the Tarahumara area with the vasiform granaries which he saw in Tlaxcala and Veracruz. There is some doubt as to its occurrence in Veracruz, however, as it is not mentioned in use in that State in the writings of Bandelier and Starr, nor is it found there at the present time. Its use in Tlaxcala and Puebla is reported by Bandelier (1884) at Huexotzingo, Santiago Xaltepetlapan and San Simon Tlalnicontla. It is Starr (1899, 1899–1900), however, who gives a complete picture of this type of granary through his descriptions and numerous illustrations. He found this granary near Cholula, Puebla, and throughout Tlaxcala. He writes (1899):

"The *cencalli* in Tlaxcala is of a characteristic form and bears the special name of *cuezcomatl*. It is a vasiform construction of adobe or of clay which rises to a height of from five to ten feet. . . . . Above this base rises the great rounded and hollow body, open above; over this a neat, little, two-pitched roof of thatch serves to shed rain. The *cuezcomatl* is a storehouse or granary for maize on the cob."

4. Log-cabin type of granary. The use of this general type of granary is reported from an extensive area in Mexico. It is found among the Tarahumara of Chi-

[1]Fanega: "The modern Spanish fanega has been equated to 1.6 English bushels, which would be slightly over 2 American bushels. For Mexico 2.5 American bushels is a conservative equivalent." (Anderson and Barlow 1943.)

huahua and the Tepehuanes of northwestern Durango (Lumholtz 1902), the farmers of Puebla, who call it *cencalli* or house of ripe corn (Bandelier 1884), and the Mixtecs at Tilantongo (Pl. XVII, A) and Yodocono, Oaxaca (Starr 1899, 1899–1900, 1908). However, several minor variations occur from place to place.

Variations to the general type are as follows:

a) the roof circular in outline; among the Triquis of western Oaxaca, in the Districts of Tlaxiaco and Juxtlahuacan (Starr 1899, 1899–1900).

b) the roof on independent pillar posts; among the Zoques at Tuxtla Gutierrez, Chiapas (Starr 1899–1900).

c) the whole structure on tall corner pillars (Pl. XVII, B); among the Mixes of Oaxaca, in the towns of Ayutla, Quesaltepec, and Ixcuintepec (Starr 1899, 1899–1900, 1908).

d) the whole structure on tall corner pillars and the thatched roof with ridge pole extending into the air (Pl. XVII, C); among the Mazatecs of Oaxaca, Districts of Cuicatlan and Teotitlan (Starr 1899–1900), and the Cuicatecs and Chinantecs of Oaxaca (Starr 1899–1900).

5. *Cincalli*, highland crib. *Cincalli* means house of maize in Nahuatl. *Cincalote*, an evident corruption of *cincalli*, is the name used by the Otomi Indians living just south of Mexico City for their crib-like granaries. As early as 1899, Starr illustrated these characteristic structures from Huixquilucan, State of Mexico (Pl. XVIII, A).

6. Cylindrical granary of upright poles and circular roof (Pl. XX, A). This type is reported among the Triquis of Oaxaca (Starr 1899–1900).

7. Maguey hut type of granary. This structure, made almost entirely from the various parts of the maguey or century plant, was found in use as a maize granary among the farmers of southern Puebla and northern Oaxaca in a markedly semi-arid area (Bandelier 1884).

8. Cylindrical or square open granaries with upright poles. This type of semi-permanent structure is reported in use among the Tepehuanes of Durango (Lumholtz 1902).

b. Temporary methods of storage

1. *Tapanco*, loft and interior of house. It seems that the following Indian groups used this method of storing maize, as no other type of granary is known among them; Tarascans of Michoacan; Zapotecs, Huaves and Chontales of Oaxaca; and Totonacs of northern Veracruz.

2. Conical container made of maize stalks (Pl. XXII, A). While describing the granaries found in Puebla, Bandelier (1884) writes:

"In the Plain, I have also seen storehouses made of cornstalks, set vertically, and tied to an inner frame, or forming a conical hollow stack. But such frail structures are temporary, and mostly used for maize only."

SUMMARY—LATE 19th CENTURY PERIOD

Granary Type	*Indian Group*	*Distribution*
A. Hacienda Granaries		
1. Conical, adobe and mortar		Aguas., Zac., Jal.
2. Cubical, stone and mortar		Tlaxcala
B. Family Maize Granaries		
a. Permanent and semi-permanent structures		
1. Niches of caves	Tarahumara	Son. and Chih.

2. Rectangular and cylindrical, stone and mortar	Tarahumara; Huicholes	Son. and Chih. Nayarit
3. *Cuezcomatl*, vasiform, grass-daub	Tlaxcalan Cholulan	Tlaxcala Puebla Veracruz (?)
4. Log-cabin	Tarahumara Tepehuanes Cholulan Mixtecs	Chihuahua n.w. Durango Puebla n.w. Oaxaca
a) circular roof	Triquis	western Oaxaca
b) roof on independent pillars	Zoques	Chiapas
c) granary on tall corner pillars	Mixes	central Oaxaca
d) granary on tall pillars with projecting ridge pole	Mazatecs; Cuicatecs; Chinantecs	northern Oaxaca
5. *Cincalli*, highland crib	Otomi	s. Mexico State
6. Completely cylindrical	Triquis	w. Oaxaca
7. Maguey hut	?	s. Pue., n. Oax.
8. Cylindrical or square open structures	Tepehuanes	Durango
b. Temporary structures		
1. *Tapanco*, loft and interior of house	Tarascan Zapotecs; Huaves; Chontoles Totonacs	Michoacan eastern Oaxaca northern Veracruz
2. Conical container, maize stalks	Cholulan	Puebla

VII. Modern Period

Many writers have dealt with the anthropological aspects of the various Indian cultures of present-day Mexico, and yet, the published material on maize granaries and methods of storing maize is very meager. The author has obtained extensive information with regard to these problems while engaged in plant exploration work in connection with the plant breeding program of the Oficina de Estudios Especiales of the Mexican Department

of Agriculture. The greater amount of this data has been obtained from the States of Tabasco, Veracruz, Chiapas, Oaxaca, Guerrero, Morelos, Tlaxcala and Puebla. It is included in this section in its proper place.

A point of special interest is the fact that not until this period is reached does the method of maize storage in the extensive area inhabited by the Mayan groups become known. This condition may be the result of the following factors: a) the lack of stimulus in this area to develop permanent granaries due to the possibility of obtaining more than one harvest of maize during the year and of replacing a shortage of maize with sweet potatoes and cassava, b) a lack of remains due to the perishable nature of the structures built for storage, and c) the tendency of archaeologists to concentrate their attention on the more spectacular elements of the Mayan civilization.

A. Permanent Hacienda Granaries

1. Cylindrical masonry structure. Eizi Matuda (in correspondence) writes that in the coffee Finca area of southern Chiapas large permanent granaries are necessary to store the supply of maize required to supply the needs of the large Indian population hired during the coffee harvest. These granaries consist of cylindrical structures made of mortar and stone. Usually a suitable slope is cut away leaving two terraces. The granary, having dimensions of 1.5 to 2 meters in diameter and 5 to 6 meters in height, is built against the intermediate wall of the terraces. This location facilitates introduction of the grain through an opening at the upper level and removal through a door located at the lower level or terrace.

B. Family Maize Granaries

a. Permanent and semi-permanent structures

1. Cylindrical stone and daub. The studies by Bennett and Zingg (1935) among the Tarahumaras of northwest Mexico include full descriptions of the maize granaries and the technique of construction. They write:

> "The cornhouses of the gorges appear to be a hold-over of the more ancient type of structure made of stone-in-mud-mortar. This type is seen in the highlands only in archaeological sites. But the cornhouses of the *barrancas* are not situated in caves. They usually stand upon large bowlders, several near a dwelling. . . . With a bowlder for a base, a circular wall of stone-in-mud-mortar is erected. It is about 4 feet in diameter and 5 feet high. Some have rather flattened fronts which contain the door."

2. *Cuezcomatl*, vasiform grass and daub. Two variations of this type are found and they are here designated as the Tlaxcalan and the Morelos forms; however, they represent a single phase of cultural development. The Tlaxcalan *cuezcomatl* (Pl. XV, B) is a vasiform structure consisting of thick walls made of grass and daub and the whole capped by a sloping flat or two-pitched roof of woven grass or of pine shingles. The entrance is through a rectangular cut made on the rim of the wall at the mouth, just below the high pitch of the roof. Maize on the cob is stored in these granaries.

The Morelos *cuezcomatl* (Pl. XV, C) is very similar except that the upper part of the structure and the roof are made of overlapping layers of grass, with an inverted clay pot often topping the apex (Linné 1938). Entrance is through a small semi-circular gable-like opening near the top. Shelled maize is stored in these granaries and removal is through a small hole close to the base. Both of these highly specialized forms of granaries are disappearing rapidly.

Luis Hernandez Xolocotzi, owner of one of the few remaining Tlaxcalan *cuezcomatls*, writes (in correspondence) that these structures are made as follows: first, a solid stone and mortar foundation is built half a meter below the ground and a half meter above; then, a good supply is made of loaf-like units, each about one meter in length, consisting of long grass stems (*Elyonurus ciliaris* HBK) well kneaded in clay; these units are placed, while still partly moist, in an overlapping fashion around and around to form the thick circular walls of the granary; finally, the wall is faced on both sides with a heavy coating of daub. He adds that formerly coiled grass cables were used to construct small *cuezcomatls*. There is no doubt, therefore, that a positive relationship exists between the archaeological granaries of the Tarahumaras, the *cuezcomatls* of the Codicis, the 19th Century reports and the modern structures of Tlaxcala and Morelos.

3. Highland log-cabin. This type of granary is found in use among the Tarahumaras of northwest Mexico and the Mixtecs of northwest Oaxaca. Bennett and Zingg (1935) give the following description of this structure:

"The most compact and carefully made structures of the Tarahumaras are the storehouses for grain, which may be as large as 10 feet high and 8 feet square. The walls are made of well-hewn boards notched to fit very closely. The foundation of these structures is usually made of beams supported by four stones to prevent moisture from entering the interior. . . . Above these floor boards, carefully notched and fitted boards are placed on edge to form the side walls in log-cabin fashion. . . . Above the walls is a ceiling (pola, Tara.), made of close-fitting boards like those used for the floor. . . . Very clever locking devices are used to prevent easy access to the interior and robbery."

The Mixtec form found near Nochistlan is very similar to the one described above. It adds a palm-thatched two pitched roof, thus providing a loft which is also utilized for storage.

4. Yanhuitlan log-cabin. This type (Pl. XVII, D) is treated separately because of its possible relationship to the pictorial representation found in the Yanhuitlan Codex. Only one of these structures was found in Yanhuitlan, Oaxaca. The walls are made of heavy pine boards with interlocking corners. The roof is of mortar and brick. A small rectangular door with a trick locking device is located high on the front wall.

5. Lowland log-cabin. Several granaries of the log-cabin type have been found at Zumpango del Rio, in central Guerrero and at Real de Guadelupe, La Parota and El Anonal in the southwestern part of Guerrero. It is the common type of granary at Zumpango where it is made of *zoyate* palm trunks (*Brahea* sp.), has a palm-thatched roof and lies close to the ground. In southwestern Guerrero, this type is found only occasionally. Here it is usually built on pillars of medium height and with a roof supported on independent posts.

6. *Cincalli*, highland crib. The present distribution of this granary, previously mentioned by Starr (1899) among the Otomi Indians, is as follows: Federal District (Isabel Kelly, in correspondence), southern Mexico State and northern Morelos at Tres Cumbres. The amount of maize harvested by a family determines the number and size of the granaries built. As the maize is consumed, the horizontal poles of the walls are taken down as far as the new level, and in this manner, by the time of the new harvest, the entire structure is practically torn down. A new structure is built each year perhaps as a preventive measure against the concentration of insects. Redfield (1930) gives the Nahuatl name as *zincolohtli*, and Starr (1899) gives the Otomi name as *cincalote*.

7. Completely cylindrical, upright poles. This is the dominant type among the Amuzgos of southeastern Guerrero. It is very similar to the structures found by Starr (1899) among the Triquis directly north of the Amuzgo area. A. Perez Toro (1922) suggests that these circular constructions indicate a cultural influence of the negro population; however, it is clearly of local origin. This type (Pl. XX, B) is reported also from Tlacotepec, Guerrero (Weitlander and Barlow 1944).

8. Maguey hut (Pl. XX, C). This structure is built much the same as a small scale model of a regular hut with a floor slightly raised above the ground and a two-pitched roof. The adaptation to the local semi-arid conditions of southern Puebla where it is used is complete, as it is built almost entirely of the different parts of the maguey plant (*Agave* spp.).

9. *Troje*, wattle and daub sealed structure (Pl. XXI, A, B). This type of granary has its main area of distribution in the State of Guerrero (entire Balsas River basin, Zumpango del Rio, and towns of "la Sierra"), although in former periods it was used over large parts of the tropical region along the Pacific coast. It is called *troje* in the lowland plains, and *cuescumal* in the upland towns. It is the most specialized and efficient type of granary found in the entire tropical region of Mexico, and its use has been extended to the storage of other crops such as sesame. Great variation exists as to shape, size and location of the *troje*, but the fundamental features of its construction are constant.

Hendriehs (1945) gives a complete illustrated description of these structures in his arresting and comprehensive study of the region formerly inhabited by the Cuicatec Indians. The main features of the granary are as

follows: the shape may be cylindrical or cubical and it may have a roof which rests upon it or upon independent supports, but in any event, it consists of thick wattle and daub walls, floor and top so that it forms a perfectly sealed unit; the body of the granary is raised some distance from the ground level; the shelled maize is poured in through a small door cut through the top wall and sealed in after all of the harvest has been stored; removal is made periodically through a small hole close to the base of the structure and, after each withdrawal, this aperture is sealed in once more with daub.

10. Cylindrical, wattle and daub open granary. This simpler type of structure is found distributed along the northern limits of Guerrero, in the Mixtec area of eastern Guerrero (Schultze Jena 1938), the northwest region of Oaxaca (I. Kelly, in correspondence), and the southwestern part of Puebla. Throughout this area it is designated as *cuescumal*, *cuescomate* and *coscomate*.

11. Tropical crib. The use of the tropical maize crib, shown in Pl. XVIII, B, C, predominates throughout most of the moist tropical areas of southern Veracruz, Tabasco, northern and southern Chiapas, Campeche, Yucatan, Quintana Roo and eastern Oaxaca. This structure has been amply described in its modern form by Lundell (1933), Wauchope (1938), Perez Toro (1942) and Morley (1946), from the Mayan area of the Yucatan Peninsula. E. Matuda (in correspondence) reports its use in southern Chiapas. I. Kelly (in correspondence) finds it aberrant among the Totonacs of northern Veracruz, while the author has seen it widely used in Tabasco and in the Chimalapa region of the Isthmus of Tehuantepec, Oaxaca.

This granary may be built within the yard of the house

or at the location of the "milpa" or maize planting. It is used to store maize in the husk and this may be thrown in haphazardly or carefully arranged in layers with the ears in a vertical or horizontal position.

12. Granary within the house. This method of storage has been found in use among the Totonacs (I. Kelly, in correspondence), the Maya of Tabasco, and the Zapotecs of the Isthmus of Tehuantepec, Oaxaca.

b. Temporary methods of maize storage

1. *Tapanco*, loft of house. This simple and effective method of storage is widely used throughout the tropical region. It is found among the Tarascans of Michoacan (D. Brand, in correspondence, G. Foster 1948), the Zapotecs of the Isthmus of Tehuantepec, Oaxaca, the Totonacs of northern Veracruz (I. Kelly, in correspondence), the Mayan groups of southern Mexico, and the farmers of the coasts of Guerrero and Jalisco.

2. *Enramada*. Throughout a large part of the coastal areas of Guerrero and Veracruz, where dry winter seasons prevail, the *enramada* serves for the storage of maize on the cob (Pl. XXI, C, D).

3. *Ziricua*, cylindrical reed container (Pl. XXII, B,C). Some variation occurs as to the kind of material used in building these containers. The most outstanding examples are found in Guerrero where they are called *ziricua* and *huatlal*. In the Balsas River Basin, the *ziricua* is usually made of stalks of *Tithonia* sp. (*acahual*, Hendrichs 1945). On the mountain slopes of Guerrero where Nahuatl-speaking groups have invaded the area, the *huatlal* is made of split bamboo canes (Hendrichs 1945). This type of granary is also found at Tixtla, Guerrero, among the Mixtecs at Cahuatachi, Guerrero (Schultze

Jena 1938), and among the Amuzgo Indians of southeastern Guerrero. The Nahuatl-speaking groups of Morelos use a similar structure called *ohuatlapilli* (Redfield 1930) made of cornstalks.

4. Non-specialized storage structures. Finally, due to the economic level of the population or to the breakdown of former patterns, several methods of maize storage which do not involve the use of specialized storage structures have been adapted in various regions. Some of these methods are: enclosures within the house, enclosures against the walls of the patio, sacks or mats, and stringers of maize ears hung on trees.

SUMMARY—MODERN PERIOD

Granary Type	*Indian Group*	*Distribution*
A. Permanent Hacienda Granaries		
1. Cylindrical, masonry		southern Chiapas
B. Family Maize Granaries		
a. Permanent and semi-permanent structures		
1. Cylindrical, stone-daub	Tarahumara	Son. and Chih.
2. *Cuezcomatl*, vasiform, grass-daub	Tlaxcalan	Tlaxcala
	Nahuatl (?)	northern Morelos
3. Highland log-cabin	Tarahumara; Mixtec	Son. and Chih. n.w. Oaxaca
4. Yanhuitlan log-cabin	Mixtec	Yanhuitlan, Oaxaca
5. Lowland log-cabin	?	central and s.w. Guerrero
6. *Cincalli*, highland crib, *cincalote*, *zincolohtli*	Otomi (?)	s. Mex. State
	Nahuatl (?)	n. Morelos, D.F.
7. Completely cylindrical, upright poles	Amuzgo	s.e. Guerrero
	?	s. Guerrero
8. Maguey hut	?	s.w. Puebla
9. *Troje*, wattle-daub sealed structure	Cuiclatec (?)	w. Guerrero
	Nahuatl (?)	n.w. Guerrero

10. Cylindrical, wattle-daub open structure	Mixtec ?	e. and n. Guerrero, n.w. Oax., s.w. Puebla
11. Tropical crib	Mayan	Yucatan Peninsula, Tabasco, Chiapas, s. Veracruz, Oaxaca
	Totonac	n. Veracruz
12. Granary within house	Mayan	Tabasco,
	Totonac	n. Veracruz
	Zapotec	e. Oaxaca
b. Temporary methods of maize storage		
1. *Tapanco*, loft of house	Tarascan	Michoacan
	Zapotec	e. Oaxaca
	Totonac	n. Veracruz
	Mayan	southern Mexico
	?	Guerrero, Jalisco
2. *Enramada*	?	Guerrero, Veracruz
3. *Ziricua*, cylindrical reed	Cuiclatec (?)	w. Guerrero,
	Nahuatl (?)	n. Gro., n. Morelos,
	Amuzgo	s.e. Guerrero
4. Non-specialized structures	?	Jalisco, Guerrero, Oaxaca, etc.

VIII. Resumen

El objecto del presente estudio es el de seguir el desarrollo de los graneros para maíz durante la historia de México, en este país adonde el maíz ha sido y sigue siendo la base principal del alimento humano. Como ya existen a la presente fecha suficientes datos para poder presentar un esquema preliminar de este desarrollo, es de esperarse que en un futuro no muy lejano se puedan establecer correlaciones significativas entre los tipos de graneros y las culturas indígenas de México. Estas correlaciones serían de gran utilidad para los investigadores agrícolas puesto que las culturas indígenas han actuado en parte como mecanismos aislantes favorables para la producción y conservación de ecotipos de maíz.

Con la introducción de este cereal a la economía agrí-

TABLE I

TENTATIVE CULTURAL AND TEMPORAL DISTRIBUTION OF MAIZE GRANARY TYPES IN MEXICO

Granary Types	Archaeological Period (500–1100 A.D.)	Pre-Conquest Period (1100–1518 A.D.)	Post-Conquest Period (1520–1600 A.D.)	19th Century Period	Modern Period
A. Large Permanent Granaries					
a. Imperial Granaries					
1. Rooms		Aztec			
2. Log-cabin		Aztec; Mixtec			
3. *Cuezcomatl*, vasiform		Aztec; Mazapan; Tlaxcalan			
4. Cask-like, wattle-daub		Aztec			
b. Encomienda Granaries					
1. Log-cabin			Mixtec		
c. Hacienda Granaries					
1. Conical, adobe-mortar				Spanish ?	
2. Cubical, masonry				Spanish ?	
3. Cylindrical, masonry					Non-Indian
B. Family Granaries					
a. Permanent and semi-permanent					
1. Subterranean	Tarahumara				
2. Niches of caves	Tarahumara	Tarahumara	Tarahumara	Tarahumara	
3. Rectangular and cylindrical, stone and mortar	Tarahumara	Tarahumara	Tarahumara	Tarahumara Huicholes	Tarahumara
4. Wattle-clay daub	Tarahumara	Tarahumara	Tarahumara		
5. *Cuezcomatl*, vasiform	Tarahumara	Tarahumara Aztec	Nahuatl	Nahuatl ?	Nahuatl ?
		Tlaxcalan	Tlaxcalan	Tlaxcalan	Tlaxcalan
		Mazapan	Mazapan	Cholulan ?	
6. Clay jars	Teotihuacan	Aztec; Cahita; Mayan ?			
7. Highland log-cabin		Aztec			
		Mixtec	Mixtec	Mixtec	Mixtec
				Tarahumara	Tarahumara
				Tepehuan	Tepehuan
				Cholulan ?	Cholulan ?
a) roof round				Triquis	
b) roof on independent posts				Zoques	
c) cabin on posts				Mixes	
d) cabin on posts and projecting ridge pole				Mazatecs Cuicatecs Chinantecs	
8. Yanhuitlan log-cabin			Mixtec		Mixtec
9. Lowland log-cabin					? Guerrero
10. *Cincalli*, highland crib		Aztec ?		Nahuatl Otomi	Nahuatl ? Otomi
11. Completely cylindrical				Triquis	Amuzgos
12. Square, upright poles				Tepehuan	
13. Maguey hut				? Puebla	? Puebla
14. *Troje*, daub-wattle, sealed					Cuiclatec ? Nahuatl ?
15. Cylindrical wattle-daub, open top					Mixtec ? n.w. Oaxaca s.w. Puebla
16. Tropical crib					Mayan Totonac
17. Granary within house					Totonac Mayan Zapotec
b. Temporary and non-specialized					
1. Rafters		Aztec			
2. *Tapanco*, loft		Cahita		Chontales Tarascan Zapotec Totonac Huaves	Mayan Tarascan Zapotec Totonac
3. *Enramada*		Cahita			?, Guerrero Veracruz
4. Conical, corn-stalks				Cholulan?	
5. *Ziricua*, reed					Cuiclatec ? Nahuatl ? Amuzgo
6. Non-specialized					? Jalisco Guerrero Oaxaca, etc.

It has not been possible to establish definite cultural determinations in every case. This fact accounts for the inclusion of such terms as Tlaxcalan and Cholulan, and for the shift from the term Aztec during the Pre-Conquest period to Nahuatl for the later periods. In the column under the heading Modern Period, wherever it has not been possible to fix the cultural element to a specific Indian group, the distribution is given.

cola de los grupos indígenas de México, estos iniciaron su época de florecimiento cultural. Pero el cultivo del maíz traía en sí involucrado el problema de su almacenamiento. Apesar de las afinidades entre los numerosos grupos indígenas, las construcciones que se desarrollaron para solucionar este problema siguieron una evalución variada que dió como resultado el sin número de formas de graneros que hoy se encuentran en las distintas regiones rurales de México.

La información sobre los graneros de maíz en México, obtenida de la literatura y las observaciones del autor, se ha dividido en cuatro épocas como sigue: I. Período Arqueologico (circa 500–1100 AD); II. Período Anterior a la Conquista (1100–1518 AD); III. Período Inmediato a la Conquista (1520–1600 AD); IV. Período del Siglo XIX; y V. Período Moderno. En cada época, se han dividido los diferentes tipos entre los comunales (tales como los del Imperio Azteca, de las Encomiendas y de las Haciendas) y los familiares (permentes y temporales). Adonde ha sido posible, se ha señalado bajo cada tipo de construcción la región adonde se encuentra y los grupos indígenas que lo utilizan. Los resúmenes bajo cada período indican la distribución cultural y geográfica de los varios tipos de graneros, mientras que la Tabla I presenta, en forma preliminar, la distribución cultural y temporal.

Los principales tipos de graneros familiares son como sigue: a) los *cuezcomatls* de Tlaxcala y Morelos; b) las cabañas de la Mixteca; c) el *cincalli* o *cincalote* de la zona elevada al sur del Estado de México; d) la *troje* de la región tropical de la Cuenca del Río Balsas, Guerrero; e) el jacal tropical de la zona Maya del sur de México; f) la *ziricua* de la región tropical de la Cuenca del Río Balsas, Guerrero; g) el *tapanco* y la *enramada* de las partes tropicales de ambas costas.

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EXPLANATION OF THE ILLUSTRATIONS

PLATE XIII. A. "Casas Grandes" archaeological remains of vasiform type of maize granary made by twisting long grass into a compact cable and laying it up one round upon another and then covering the wall with thick coats of plaster on inside and outside; Tarahumara Indians of Sonora and Chihuahua. B. "Casas Grandes" archaeological remains of vasiform type of maize granary; Tarahumara Indians of Sonora and Chihuahua. (A and B reproduced from C. Lumholtz 1902.)

PLATE XIV. A. Imperial granaries of the log-cabin type depicted in the Codex Mendoza as units of measure of the tribute required of the various conquered towns by the Aztec rulers during the pre-Conquest Period; figs. 21 and 22 show two of these structures, with representations of maize, beans and *quautli* (*Amaranthus caudatus*) seeds above; town glyph number 6 represents Cuezcomahuacan. B. *Cuezcomatl*, vasiform grass and daub granary used by the agricultural families of the Aztec Indians during the pre-Conquest period. The glyph of the conquered town number 11 shows this type of structure and signifies Cuezcomatlyyacac or "in the beginning of the granaries." C. *Cuezcomatl*, vasiform grass and daub granary depicted in the glyph of Cuezcomayxtlahuacan, conquered town number 19 and interpreted as "the place of the plain of bins." (A, B and C reproduced from the Codex Mendoza, Kingsborough 1831–1848.) D. *Cuezcomatl*, vasiform granary used by the Aztec Indians during the pre-Conquest period as shown in the Codicis; the glyph corresponds to the town of Cuezcomatl Iyacac. (Reproduced from the Historia Chichimeca, Boban 1891.)

PLATE XV. A. *Cuezcomatls*, vasiform maize granaries used by the farmers of Tlaxcala during the later part of the 19th Century. (Reproduced from Starr 1899.) B. Tlaxcalan *cuezcomatl*, vasiform type of maize granary used at present in decreasing numbers among the farmers of Tlaxcala; found at San Bernabe Amaxac de Guerrero, Tlax. C. Morelos *cuezcomatl*, vasiform granary used to store shelled maize; entrance is through the small gable-like opening near the top; the apex is usually terminated by an inverted clay pot.

PLATE XVI. A. storage of maize in large clay jars among the Aztec Indians during the pre-Conquest period. B. Highland log-cabin type of granary used by the Aztec Indians during the pre-Conquest period; note that the ears of maize shown are very similar to the Mexican pyramidal race which is still dominant in the area near Mexico City today. (A and B reproduced from Sahagun 1529–1590.)

PLATE XVII. A. Log-cabin type of family granary used by the Mixtec Indians of Tilantongo, Oaxaca during the later part of the 19th Century. B. Log-cabin type of family granary used by the Mixe Indians of Oaxaca during the later part of the 19th Century; the entire structure is built on four corner pillars of medium height. C. Log-cabin type of family granary used by the Mazatec Indians of Huautla, Oaxaca during the later part of the 19th Century; the entire structure is built on tall corner pillars, and the projecting ridge poles of the roofs are very characteristic. (A and C reproduced from Starr 1908; B from Starr 1899.) D. Yanhuitlan log-cabin type of family granary very similar to the ones depicted in the Yanhuitlan Codex; found rarely at present among the Mixtec Indians of Yanhuitlan, Oaxaca.

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PLATE XIX. A. Hacienda granaries, conical adobe-mortar type found over a small area of Zacatecas, Aguascalientes and eastern Jalisco; photograph shows the spiral stairways leading to the aperture near the apex. B. Hacienda granary, conical adobe-mortar structure showing the outlet door at the base. (Photographs by Dr. P. C. Mangelsdorf.)

PLATE XX. A. Completely circular structure used for storage of maize by the Triqui Indians of Oaxaca during the later part of the 19th Century. (Reproduced from Starr 1899.) B. Completely circular maize granary used by the Amuzgo Indians of southeastern Guerrero; Modern Period. C. Maguey hut type of maize granary used at present by the farmers of southeastern Puebla; the entire structure with the exception of the corner posts is made from different parts of the maguey plant (*Agave* sp.). (Photograph by Dr. P. C. Mangelsdorf.)

PLATE XXI. A. *Troje*, wattle and daub sealed structures used to store maize at present in the tropical lowland area of the Balsas River Basin, Guerrero; the photograph shows the first steps in the construction of this type of structure. B. *Troje*, wattle and daub sealed structures; photograph showing the application of the daub on the inner walls; Balsas River Basin, Guerrero. Modern Period. C. *Enramada*, temporary structure used for maize storage over a large part of the tropical coastal areas of Mexico where dry winter months prevail; near Petatlan, Guerrero. D. *Enramada*, variant form used at present near Veracruz City, Veracruz. (Photograph by Dr. P. C. Mangelsdorf.)

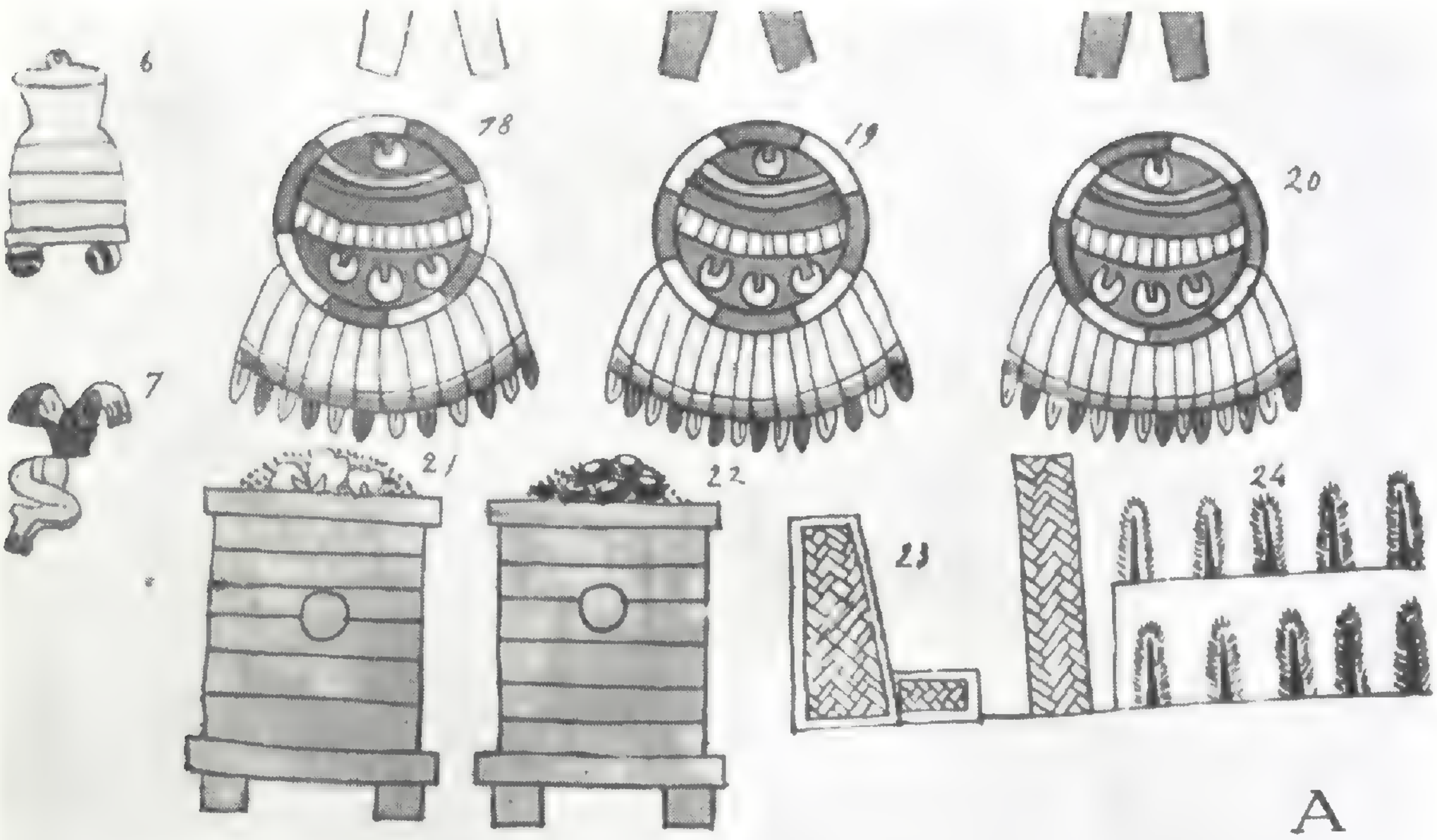
PLATE XXII. A. Temporary conical structure made of maize stalks and used for maize storage near Cholula, Puebla, during the later part of the 19th Century. (Reproduced from Starr 1899.) B. *Ziricua*, temporary structure made of maize stalks and used by the farmers of the Balsas River Basin, Guerrero for storage of maize. Modern Period. C. Cylindrical reed structure similar to the *ziricua* and used at present for maize storage among the Amuzgo Indians of southeastern Guerrero.

Plate XIII

A

B

Plate XIV



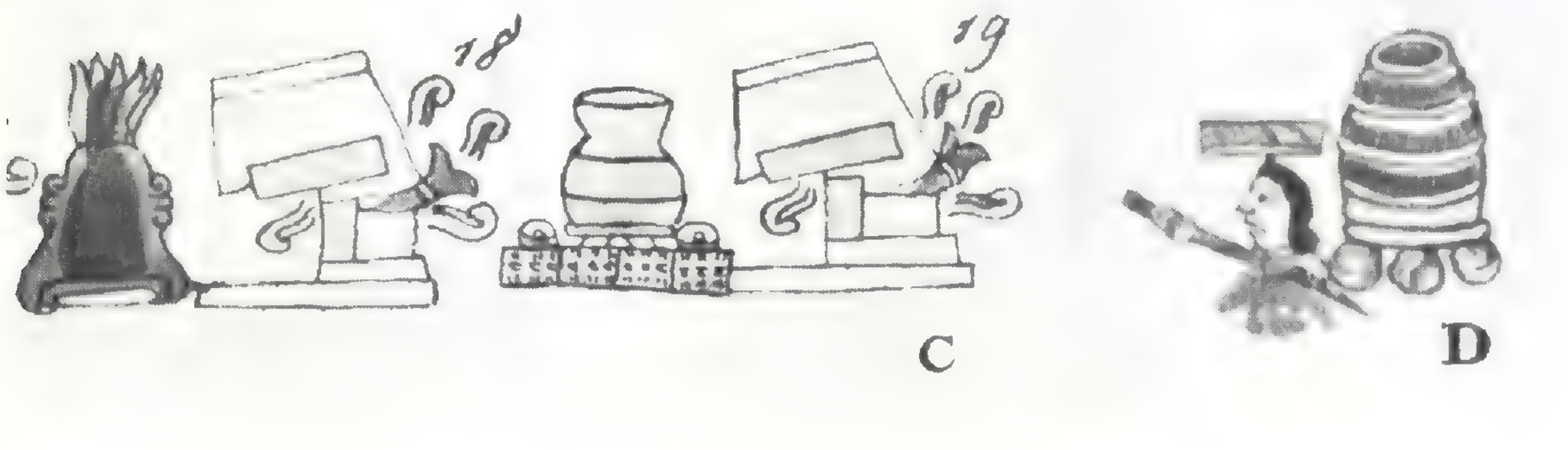


Plate XV

Plate XVI

Plate XVII

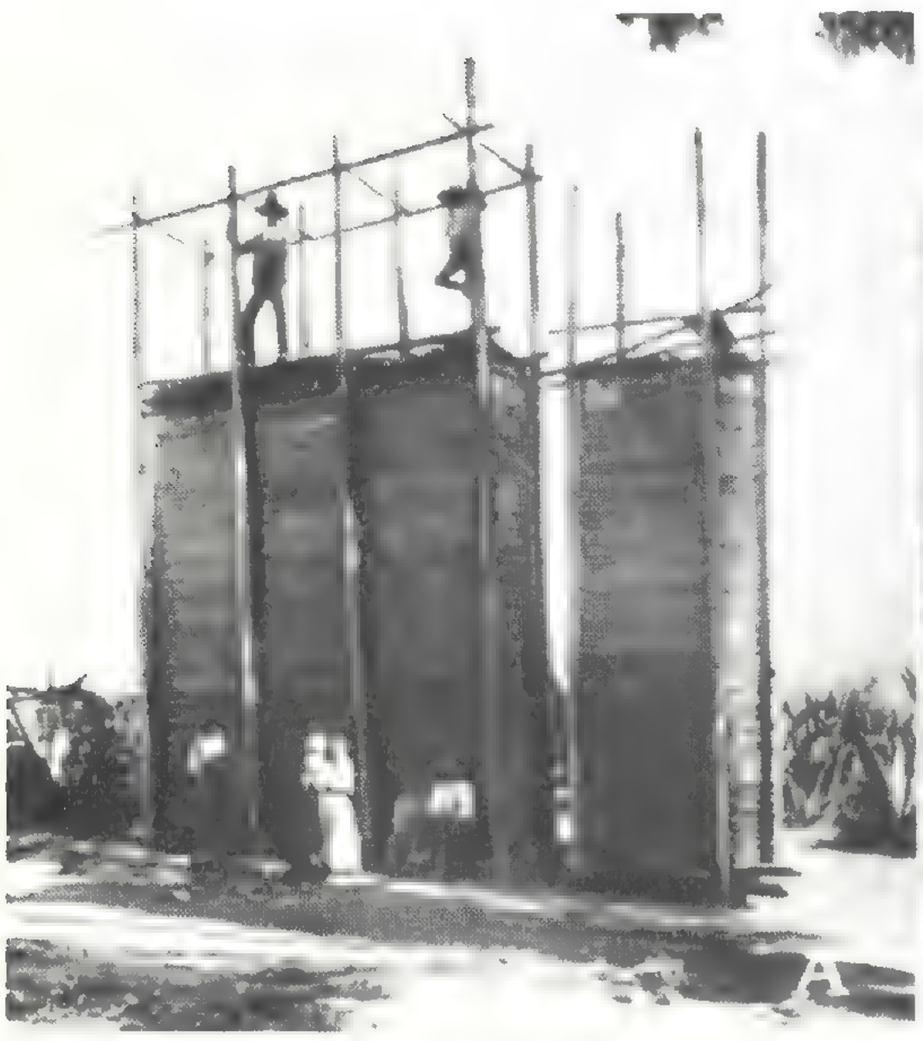
A

B

C

D

Plate XVIII


A

B

C

Plate XIX

A

B

Plate XX

Plate XXI

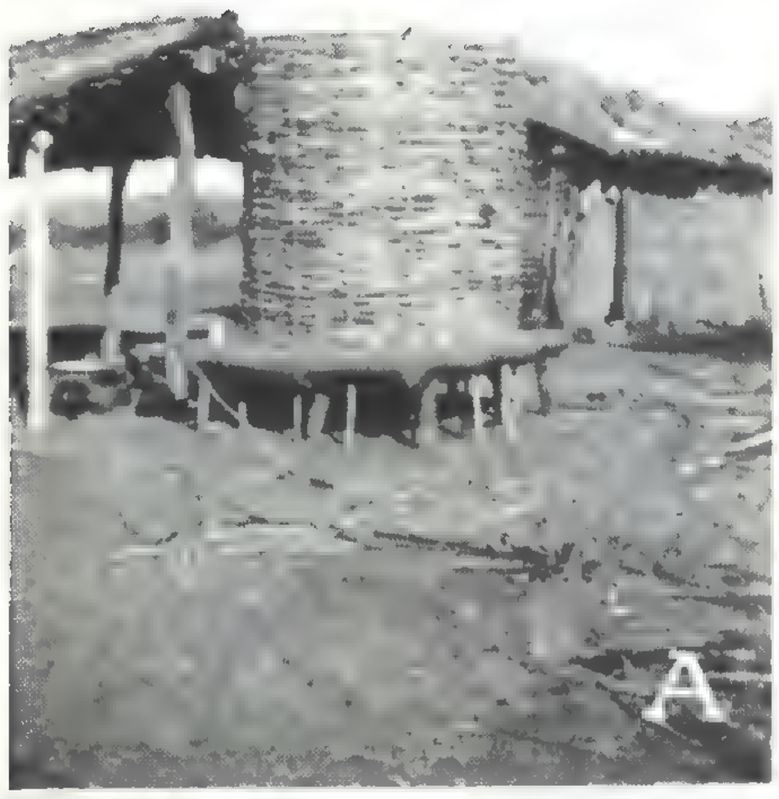
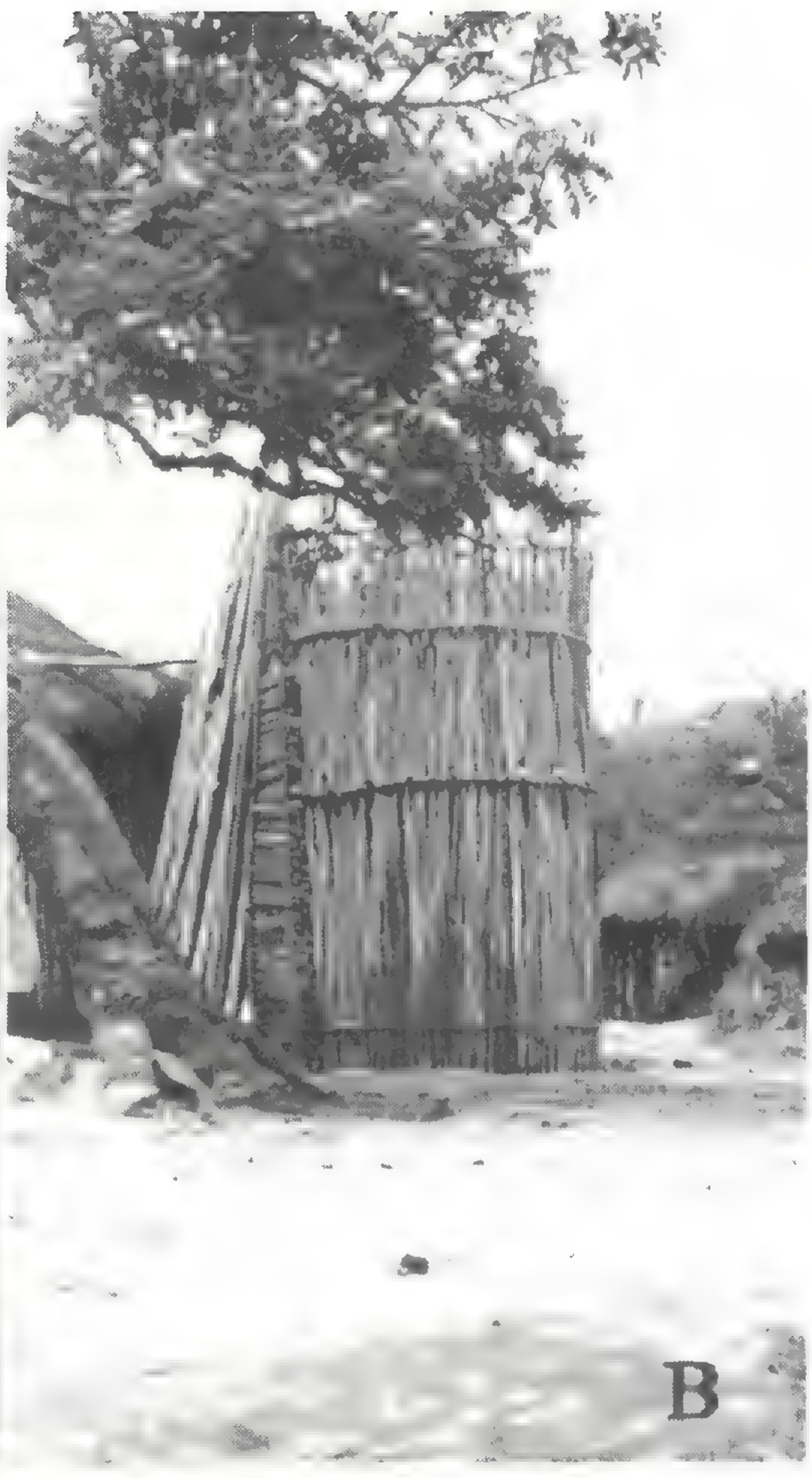


Plate XXII

A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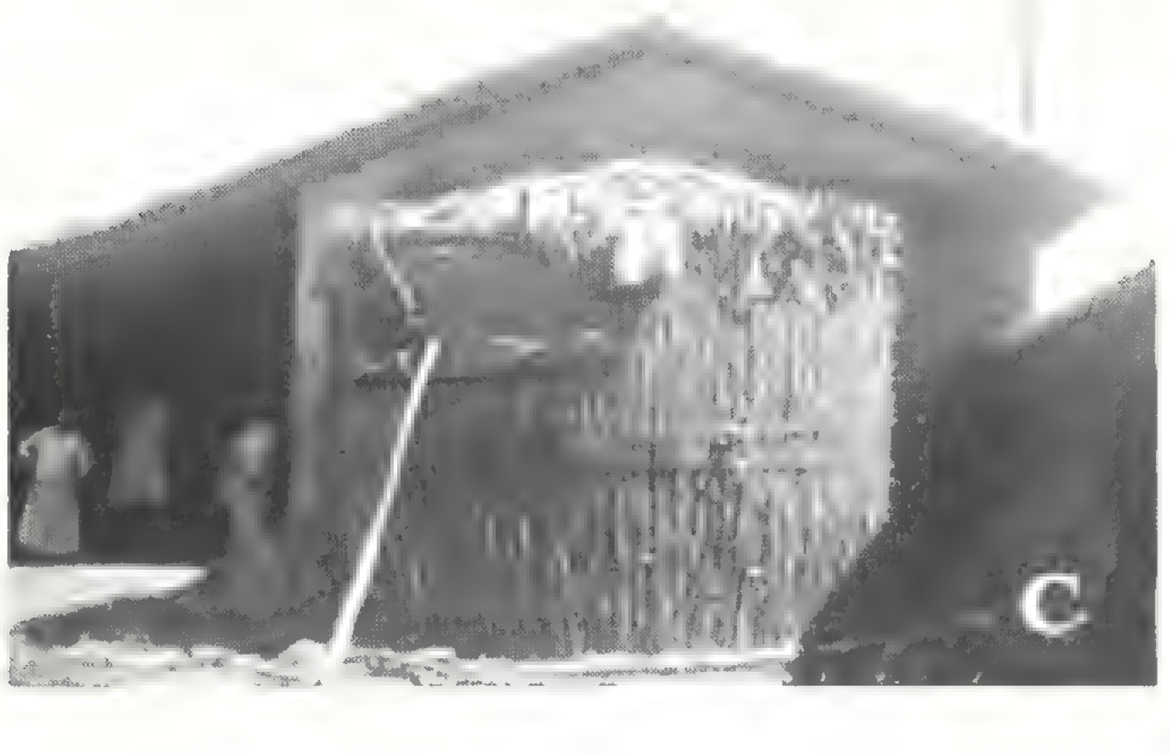
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BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, MARCH 4, 1949 VOL. 13, NO. 8

NEW ARCHAEOLOGICAL EVIDENCE ON EVOLUTION IN MAIZE

BY

PAUL C. MANGELSDORF AND C. EARLE SMITH, JR.

THE problem of the origin of maize, which for several generations past has commanded the attention of botanists and archaeologists alike, is appreciably nearer the point of final solution as a result of the discovery of important prehistoric plant remains in New Mexico during the summer of 1948. An expedition sponsored by the Peabody Museum of Harvard University[1] and led by Mr. Herbert W. Dick, a graduate student in anthropology, uncovered many cobs and other parts of maize from the accumulated refuse in an abandoned rock shelter, known as Bat Cave. This material not only furnishes direct proof of the nature of primitive maize but also provides for the first time tangible evidence of a well-defined evolutionary sequence in this important American cereal.

Anticipating the evidence to be presented in detail later in this paper, it can be said here that direct archaeological evidence is now available to show: (1) that primitive maize was both a pod corn and a pop corn; (2) that

[1] This expedition, the Early Man Division of the Upper Gila Expedition of the Peabody Museum of Harvard University, is under the general direction of Dr. J. O. Brew and is financed in part by the Viking Fund of New York City; the excavation of Bat Cave was in cooperation with the University of New Mexico. The general aims of the Expedition are set forth by Brew and Danson (1948).

maize did not originate from teosinte; (3) that much of the variation in modern maize is the product of introgression from teosinte which occurred as a later step in the evolution of maize.

The prehistoric maize remains which permit us to draw these far-reaching conclusions comprise a considerable part of the total vegetal remains isolated from the refuse in Bat Cave by Mr. C. Earle Smith, Jr., the junior author of this paper, who served as botanist to the expedition. The vegetal remains other than maize, which are also of considerable ethnobotanical interest, will be described separately by Mr. Smith. Suffice it to say here that, in addition to maize, seeds of both kidney beans and squashes were found at all except the lowest levels of the Bat Cave refuse in which maize itself occurs.

Description of Bat Cave

Location and Climate. Bat Cave is located in Catron County, New Mexico, on the edge of the Plains of San Augustin, the basin of an ancient lake of considerable size which has been described by Powers (1939). The longitudinal axis of the basin which lies in a northeast to southwest direction is about 60 miles. The basin varies from six to twenty miles in width.

There are no natural streams permanently flowing into the basin and the plains are dry for the better part of the year. The arroyos and canyons carry water only during the rainy season in July and August, when afternoon showers sometimes precipitate large amounts of water in a short period of time. Records kept at Aragon, a village about 25 miles from the site, indicate an average annual rainfall of approximately 14 inches; the precipitation, at present, on the plains of San Augustin, is probably a few inches less.

Present Vegetation. The paucity of water in the re-

gion greatly restricts the natural vegetation. In the immediate vicinity of the site at Bat Cave *Atriplex canescens* (Pursh) Nutt. provides the major cover on the plain with species of Sporobolus and Heliotropium playing a secondary rôle. There is a distinct change in the vegetation as one leaves the old lake floor and ascends the gravelly beach terraces which mark the ancient shores of the lake. Russian thistle, *Salsola pestifer* A. Nels., is common on the edge of the plain. Many species of Compositae, Labiatae, Chenopodiaceae, Amaranthaceae, Boraginaceae and Gramineae are found on the terraces themselves. Where the terraces are especially rocky, *Fallugia paradoxa* (D. Don) Endl. occurs as a common shrub with *Rhus trilobata* Nutt. ex Torr. & Gray and species of Ribes and Forsteria. During the dry season this vegetation has a distinctly xerophytic appearance accented by occasional plants of Opuntia and Mammillaria. In the rainy season the vegetation becomes quite green, and a number of short-lived annual flowering plants, as well as species of Selaginella and Notholaena, make their appearance.

The vegetation remains more or less the same for some 200 to 400 feet up the slopes surrounding the basin. At this point a distinct change in the vegetational pattern occurs. *Pinus edulis* Engelm. and *Juniperus* spp. become the dominant features in the vegetation. In one canyon near Bat Cave several trees of *Pinus ponderosa* Dougl. ex P. Laws. occur, while, in some protected areas of this piñon-juniper belt, trees of various species of Quercus are found.

Vegetation in the Past. The species identified among the vegetal remains found in Bat Cave would seem to indicate that the natural vegetation which occurs today is not substantially different, except in a few character-

istics, from that of the past. The region is not one where such plants as maize, beans and squashes, none of them species notable for drought resistance, would be expected to occur in the wild, and certainly at the present time conditions are scarcely suitable for their cultivation. At an earlier period, however, when Lake San Augustin was a permanent body of water with a water level considerably higher than the present level of the plain, maize, beans and squashes could have been, and undoubtedly were, grown on its shores.

Description of the Site. Bat Cave is situated on the eastern edge of the Plains of San Augustin about 165 feet above the level of the lake floor and at an altitude of about 7000 feet. Carved out of an almost vertical cliff, apparently by wave action, Bat Cave is actually a series of six more or less separate caves. The largest of these is about 100 feet deep and 75 feet from floor to roof. A second is approximately 40 feet deep and 30 feet from floor to roof. Four smaller caves lying between these two are 10 to 20 feet deep and 10 to 15 feet high. It is from these smaller caves that the material described in this paper was excavated.

Excavation of Material. The refuse was removed in successive strata each about twelve inches in thickness. The lowest stratum which contained plant remains is designated as I and the uppermost as VI.

The bulk of the material was carefully excavated *in situ* by hand trowelling on a vertical face. The depth of the specimen was carefully noted in all cases. All the botanical material was packaged in separate lots for each area in the excavation.

The total depth of the deposits in which maize was found averaged between five and six feet. The entire

deposit bore artifacts without hiatus to the bottom where it rested upon a layer of water-washed gravel.

Dating. Dr. Ernst Antevs, who is preparing a separate report on the geology of Bat Cave and the surrounding region, estimates that the cultural deposits containing the maize had their beginning not later than 2500 B.C. This estimate is based on the fact that the refuse rests upon a layer of windblown sand and dust which represents a period decidedly drier than the present. Antevs believes the sand and dust were deposited between 5500 B.C. and 2500 B.C. The level representing this very dry age rests upon old beach gravels which were laid down during a preceding pluvial period. The gravel rests on bedrock. The top level of the maize-bearing deposit is dated by pottery as 500 A.D. to 1000 A.D. Thus, the deposit containing maize covers a span of not less than 3000 years. Exact dating of the site is not, for our purpose, of overwhelming importance. Much more significant is the fact that the characteristics of the maize from Bat Cave are such as to make it the most primitive which has so far been discovered; and, even with conservative dating, it is the most ancient.

Maize Remains. The maize remains isolated from the refuse comprised a total of 766 specimens of shelled cobs, 125 loose kernels, eight specimens of husks, ten of leaf sheaths, and five of tassels and tassel fragments. Most of the specimens, even those from the lowest stratum, were extraordinarily well-preserved, with the long plant hairs on the epidermis of the glumes and the surface of the cupules still intact. Indeed, most of the vegetal material is in such an excellent state of preservation that botanists would be inclined to question the geologists' estimates of its antiquity did not the specimens of maize from the different strata exhibit a distinct evolutionary sequence.

The Evolutionary Sequence in the Cobs

Shelled cobs comprised by far the largest fraction of the maize remains found in Bat Cave. These included 52 separate lots, totaling, as has already been stated, 766 specimens. Of these, 471 were sufficiently well-preserved to be studied for a number of distinct botanical characteristics.

Our method of studying the prehistoric cobs was to snap each cob in two, examining the two surfaces thus exposed under a dissecting microscope. The number of characteristics which can be studied in the maize cob is truly astonishing. Those which we considered are listed in Table I. Further studies of the maize cob will undoubtedly reveal other characteristics which can be utilized in comparing maize populations. Lenz (1948), for example, describes a "rachis flap" which is prominent in some varieties and relatively inconspicuous in others. The rachis flap was so erratically distributed in the Bat Cave specimens that we gave no serious attention to it. Nor did we attempt to measure rachilla length, another characteristic in which maize varieties differ considerably, according to Lenz (1948) and Cutler and Cutler (1948). However, some of the other characteristics which we did investigate, such as length and shape of the glumes, are strongly correlated with rachilla length, so that indirectly we undoubtedly took this character into account.

The characteristics in which the specimens from the six strata are compared are described below.

Length of Cob. This is a simple measurement made on all cobs which were intact with respect to length or so nearly intact that their original length could be estimated. The data in Table I show that there is little difference in the mean length of the cobs in the first three strata. Thereafter, there is a more or less progressive in-

TABLE I. CHARACTERISTICS OF THE PREHISTORIC MAIZE OF BAT CAVE COMPARED BY STRATA

	Characteristics		*Stratum* I	II	III	IV	V	VI
	No. of separate lots		2	4	8	6	8	24
	Total No. of cobs		25	55	77	146	118	345
	No. cobs scored		19	23	38	75	78	238
	No. cobs intact in length		4	2	5	13	17	25
	Length intact cobs—cm.	max.	9.5	10.3	9.5	13.8	15	16.5
	" " " "	min.	6	7.2	6.5	5.1	5	4
	" " " "	mean	7.3	8.4	7.7	8.5	9.6	9.3
	Mean diameter of rachis	mm.	7.5	8.6	7.9	8.4	9.9	11.2
	" " " cob	"	14.8	15.7	15.3	16.2	17	17.5
	Index cob/rachis—max.		2.5	3	2.8	2.6	2.5	2.8
	" " " min.		1.6*	1.5	1.4	1.2	1.2	1.2
	" " " mean		1.9	1.8	1.9	1.9	1.7	1.6
	Rows of grain—max.		14	16	16	20	16	20
	" " " min.		8	8	8	4	8	4
	" " " mean		10.7	12	11.2	12	11.6	11.4
	Rachis tissue	% spongy	28	88	58	43	29	38
	" " "	horny	72	12	39	39	28	24
	" " "	bony			3	18	43	38
	Surface of cupules	% glabrous	19	4	8	8	8	22
	" " "	" hispid			3	13	25	15
	" " "	" hirsute	81	96	89	79	67	63
Lower Glumes	Texture	% fleshy	97	91	71	56	25	40
		" horny	3	9	26	36	18	21
		" bony			3	8	57	39
	Surface	" glabrous	100	96	95	79	92	85
		" hairy		4	5	21	8	15
	Venation	" slight	10	44	18	51	6	16
		" none	90	56	82	49	94	84
Upper Glumes	Shape	% boat	20	13	16	12	7	8
		" intermed.	80	61	47	59	38	49
		" collar		26	37	29	55	43
	Texture	" chaffy	100	48	47	61	37	49
		" fleshy		52	53	39	59	48
		" horny					4	3
	Surface	" glabrous	100	96	89	71	74	78
		" hispid			3	8	3	3
		" hairy		4	8	21	23	19
	Venation	" strong	30	30	29	56	21	26
		" intermed.	53	26	55	28	41	43
		" none	17	44	16	16	38	31
	Tunicate alleles	% tu					1	
	" " "	" tu^w			8	1	33	55
	" " "	" tu^f	80	92	82	73	61	42
	" " "	" tu^h	20	8	10	26	5	3
	Teosinte introgression	% none	100*	100‡	73	43	9	27
	" "	% intermed.			22	52	58	61
	" "	% strong			5	5	33	12
Kernels	Total No.		2	2	10	20	67	24
	Av. length	1/1000 in.	275	293	280	312	302	316
	Av. thickness	" "	193	247	223	210	236	217
	Width max.	1/1000 in.	258	301	340	376	398	428
	" min.	" "	230	229	213	214	197	201
	" mean	" "	244	265	265	284	308	333

* There is one cob with a cob/rachis index of 1.2 which also shows evidence of strong introgression of teosinte. Since this cob is atypical of the stratum in other characteristics as well it is undoubtedly an intrusion and is not included in this datum.

‡ There is one cob in this stratum which shows unmistakable teosinte introgression but which is atypical in other respects and is probably an intrusion.

crease in mean length from stratum to stratum. Even more interesting than the mean length of the cob is a comparison of the maximum and minimum lengths. Beginning with the fourth stratum there is a progressively greater divergence between the shortest and the longest ears in each stratum. Part of the increase in range of variation may be attributed to a progressive increase in the size of the samples available, but there is no doubt that there is a true increase in the range of variation beyond that resulting from sampling. This is reflected not only in the size of the cob but in many other characters as well.

Diameter of the Rachis and Cob. When a cob of maize is snapped in two it is quite easy, in examining the cross section, especially of the lower half, to distinguish between an inner zone made up of the rachis and an outer zone made up of the glumes. These zones represent two concentric circles whose diameter is easily determined with a pair of calipers. The data in Table I reveal that there are no significant differences in the diameters of the rachis and the entire cob in the three lowest strata. Thereafter, however, there is a progressive increase in mean diameter of the rachis and in mean diameter of the entire cob from stratum to stratum.

The Cob/Rachis Index. Much more important than the actual diameter of these two concentric circles representing the rachis and the entire cob is the ratio of one to the other. This ratio, called the cob/rachis index and obtained by dividing the larger figure by the smaller, may prove to be one of the most useful measurements yet employed in studying and classifying maize varieties, for it has a clear-cut and definite genetic basis involving changes in alleles at the *Tu-tu* locus on the fourth chromosome. The existence of four alleles—tunicate (*Tu*),

half-tunicate (*tu*^{h}), weak-tunicate (*tu*^{w}), and non-tunicate (*tu*)—at this locus has already been demonstrated (Mangelsdorf, 1948). In addition, a condition intermediate between weak-tunicate and half-tunicate is found in some races of maize including the Chapalote maize of Mexico. Since this form of tunicate, which has not yet been studied genetically, produces approximately the same effect when homozygous as does half-tunicate when heterozygous, it may appropriately be called fourth-tunicate and tentatively given the symbols *tu*^{f}, subject to verification by later genetic tests.

The importance of these *Tu* alleles in connection with our present studies lies in the fact that a change from a higher to a lower allele in the series is almost invariably accompanied by a drastic change in the cob/rachis ratio. In other words, when the glumes become shorter, the rachis, other factors remaining constant, automatically becomes thicker. This is easily demonstrated in modern isogenic stocks which are segregating for two alleles in the *Tu* series. A comparison of three such stocks is shown below:

Stock	*Cob/Rachis Index*
Inbred A158 *tuhtuh*	2.9
" " *tuhtu*	2.1
" " *tutu*	1.5

The cob/rachis index, therefore, is in substantial part a simple estimate of the degree to which a variety of maize has departed from a primitive tunicate form toward the modern non-tunicate condition. It must be realized, however, that in addition to changes in both the diameter of the rachis and that of the entire cob resulting from changes in *Tu* alleles, there are other differences resulting from the action of a vast number of modifying factors.

It is interesting to note that the cob/rachis index in the Bat Cave maize varies from 3.0, a condition in which the rachis is slender and the glumes are prominent, to 1.2, a condition in which the rachis is large and the glumes are relatively short. The cob/rachis index is, however, relatively constant through the three lower strata, but shows some change in the upper three. It is of particular interest to note that, although new types with a low cob/rachis index appear in the upper strata, the original types with a high index, though becoming somewhat less frequent, do not disappear. If human selection had been operating in favor of the lower alleles at the *Tu-tu* locus, it certainly had not, in the period represented by the uppermost strata, succeeded in completely eliminating the higher alleles. There has, as in other characteristics, been primarily an increase in the range of variation.

Rows of Grain. There has been no constant change in the number of rows of grain from stratum to stratum. An increase in the circumference of the cob should result either in an increased number of rows of grain or in wider grains. It will be shown later that there has been a progressive increase from stratum to stratum in the average width of the grains. Similarly, although it is not clearly revealed by the summarized data, there has been an increase in the number of rows as a consequence of the increase in the circumference of the rachis. Indeed, the principal variation in the two lower strata has been concerned largely with the diameter of the rachis, the prominence of the glumes and the number of rows. Of 41 ears which were scored for both row numbers and *Tu* allele, 16 were classified as fourth-tunicate, 8 as half-tunicate and 17 as intermediate between these two conditions. The average row numbers of these three groups is shown below.

Type of Ear	*Average Row Number*
Half-tunicate	10.5
Intermediate	11.2
Fourth-tunicate	11.9

Here, then, is another factor not previously recognized which is involved in the complex problem of row number in maize. It can now be said that, other things being equal, the lower the allele of *Tu*, the higher will be the number of rows on the ear.

Rachis Tissue. It is a common observation both of practical farmers and students of maize that there is a great variation in the hardness or stiffness of individual cobs. Lenz (1948) has recently reported that the texture of the cob depends to a large extent upon the relative amount of heavily schlerenchymatized tissue. A histological examination of the nearly 500 cobs included in this study was out of the question, but it was possible to score the cobs with respect to the tissue of the rachis by testing with a dissecting needle the surface exposed when the cob was broken. The tissue immediately below the epidermis of the rachis was used for this purpose; the cobs were classified as having spongy, horny or bony tissue. Bony cobs, such as would be expected from an introgression of Tripsacum or teosinte, do not make their first appearance until Stratum III where they occur to the extent of three percent. The percentage of bony cobs reaches a maximum of 43 percent in Stratum V and falls off slightly to 38 percent in Stratum VI.

Surface of Cupules. The alveoli or cupules in the rachis from which the paired spikelets arise vary considerably in the nature of their surfaces. Some are virtually glabrous, others are beset with short stiff hairs (hispid) and still others are lined with long slender hairs (hirsute). Glabrous and hirsute types occur in all strata, but cupules

with hispid surfaces do not make their appearance until Stratum III. Thereafter, they increase progressively to Stratum V and fall off again in VI, a pattern quite similar to that exhibited by bony cobs and probably for the same reason. A strong introgression of teosinte into maize, as in some segregates from maize-teosinte hybrids, results in glabrous cupules. This is not surprising, since the inner surface of the bony shell of teosinte, the counterpart of the cupule in the rachis of maize, is always glabrous. But a smaller amount of teosinte introgression may cause the hairs in the cupule merely to be shorter and stiffer. Thus the hispid condition encountered in later strata of the Bat Cave material may well be a manifestation of teosinte (or Tripsacum) introgression.

Lower Glumes. The lower glumes of an ear of maize vary: (a) in texture which may be chaffy, fleshy, horny or bony; (b) in surface which may be glabrous, hispid or hairy; and (c) in venation which may be apparent to the eye or obscured by the thickness of the tissues. The data in Table I reveal that there are no truly chaffy or membranaceous glumes such as are found in modern pod corn. Neither are there bony glumes such as those found in teosinte until we reach Stratum III. Thereafter, the percentage of bony glumes increases progressively to Stratum V and falls off slightly in Stratum VI. The induration of the glumes is almost a certain sign of teosinte or Tripsacum introgression. Types with bony glumes similar to those found in the upper strata of this material are readily synthesized experimentally by substituting one or more chromosomes from teosinte for the corresponding maize chromosome. There is little doubt that the strong, bony glumes evident in much of the Bat Cave material is the product of introgression from teosinte or

Tripsacum. The significant fact is that this introgression is not apparent in the lower strata.

The fact that all glumes in the lowest stratum are glabrous may be of some significance. Cutler and Cutler (1948) report that hairs on the pistillate glumes are occasionally present in numbers proportional to those found on the leaf sheath. Insofar as glabrous pistillate glumes are associated with glabrous leaf sheaths, we may infer that the early Bat Cave corn was glabrous. Completely glabrous husks, found in Stratum II and described later, support this conclusion.

The venation of the lower glume may be obscured because the glume is fleshy or because it is indurated as in teosinte. Both conditions are encountered in this material. Glumes on 90 percent of the ears in the lowest stratum show no venation because they are fleshy. In Stratum VI, however, the lack of venation occurs on both fleshy and indurated glumes.

Upper Glumes. The upper pistillate glumes, easily studied on the exposed end of the lower half of a broken cob, possess several interesting characteristics. They vary in shape from those which resemble one end of a boat and have obviously once enclosed a kernel, to a short, stiff half-collar which once surrounded the base of a kernel. Forms intermediate between these two extremes are common. Boat-shaped upper glumes characteristic of true pod corn are found in all six strata, but are most common in Stratum I. Collar-shaped glumes are most common in Stratum V.

The upper glume is most commonly membranaceous or chaffy, but may be fleshy, and, as in teosinte and Tripsacum, even horny. All of the ears in the lowest stratum have chaffy upper glumes. Horny upper glumes occur only in Strata V and VI.

The surface of the upper glumes, like that of the lower, may be glabrous, hispid, or hairy, although the two glumes are not necessarily identical with respect to these characteristics. Only glabrous upper glumes were found in Stratum I and glabrous glumes continued to predominate throughout all strata. Hairy upper glumes made their first appearance in Stratum II and increased in frequency in successive strata up to V. Hispid upper glumes first appeared in III and occurred in small percentages in the remaining strata.

The visible venation of the upper glume is strongly but not completely correlated with its shape and texture. The data on venation of the upper glume in this material are generally in agreement with the data on shape and texture. Strongly veined glumes, like those which are boat-shaped or chaffy, have their lowest frequency in Stratum V.

Tunicate Alleles. An attempt was made to classify the cobs with respect to the degree to which they were tunicate or non-tunicate. As has already been mentioned, four degrees of tunicate—*Tu*, *tuh*, *tuw*, and *tu*—are known and a fifth, *tuf*, intermediate between *tuh* and *tuw*, is believed to occur.

No cobs with glumes as strongly developed as those of modern pod corn of the genotype *Tutu* were found, but true pod corn of the half-tunicate type occurred in each of the six strata. Pod corn of the fourth-tunicate type also occurred in all strata and indeed was the most common type in all except the uppermost. Weak-tunicate first appeared in Stratum III and became the most common type in VI. Only one ear regarded as non-tunicate was encountered.

These data indicate strongly that one of the principal factors involved in the evolution of maize has been a

gradual replacement of the higher alleles in the *Tu-tu* series by the lower. Mangelsdorf (1948) has shown that both *Tu* and *tuh* have relatively high mutation rates. It is evident from the Bat Cave material that mutations at the *Tu-tu* locus have occurred and that there has been a gradual decline in the frequency of the higher alleles and an increase in the frequency of the lower. This, in turn, has had far-reaching effects upon the size of the rachis, on the size of the entire cob, on the space available for the vascular system, upon the length of the rachillae which bear the kernels and undoubtedly upon the ultimate yield of grain. The importance of the changes in relative frequency of the different *Tu* alleles can scarcely be over-emphasized.

Teosinte Introgression. The hypothesis of Mangelsdorf and Reeves (1939) with respect to the origin of maize postulates that teosinte is the product of a natural hybridization of maize and Tripsacum which was followed by an introgression of teosinte (or Tripsacum) germplasm into maize. The origin of teosinte as the progeny of maize and Tripsacum has not yet been finally proved, although much additional evidence in support of the hypothesis has been accumulated since 1939 (cf. Mangelsdorf, 1946). For the purpose of this paper, however, it is not necessary to debate the question of the origin of teosinte. We are here concerned primarily with the question whether there is evidence of such an introgression of teosinte into maize. The answer is that there is strong evidence of such introgression, but only in the later strata of the Bat Cave material.

The scores for teosinte introgression represent estimates involving personal judgment which in turn is based upon an extensive experience in studying derivatives of maize-teosinte hybrids produced experimentally. When

a cob has bony rachis tissue, bony lower glumes, upper glumes lacking in venation and a hispid cupule, it is almost certainly a product of teosinte introgression. If it has some of these characteristics, but not all, it is assumed to represent teosinte introgression of a lower order.

In each of the first two strata there was only one cob which showed evidence of strong introgression of teosinte. These cobs were atypical of the strata in almost all of their characteristics and are probably "intrusions," a convenient term employed by archaeologists to describe specimens which are found in any part of a cultural deposit in which they obviously do not belong. With rats and other rodents digging burrows in ancient refuse heaps, it is almost inevitable that a specimen from a higher stratum will occasionally find its way into a lower. Intrusions, therefore, have a real basis in fact and are not merely a device for conveniently explaining exceptions.

Cobs showing evidence of teosinte introgression occur in somewhat greater frequency in Stratum III, but are not common. These, too, may be intrusions or they may result from the fact that the line of demarcation between the strata is entirely arbitrary. In any case, not until Stratum IV is reached can we be certain that teosinte-contaminated maize has become a conspicuous part of the population.

The amount of teosinte introgression is greatest in Stratum V and drops off perceptibly in Stratum VI. Two possible reasons for this decline come to mind at once. The first is that introductions of non-tripsacoid maize from other regions have "diluted" the teosinte germplasm; the second is that some of the more obvious effects of teosinte have become modified through the development of an appropriate modifier complex. Since there is no clear-cut evidence of an introduction of non-tripsacoid maize on a large scale, the second possibility

appears to be the more plausible one. The senior author (1946) suggested several years ago that much of the recent evolution in maize has been a matter of absorbing the morphological assets of teosinte while suppressing its morphological liabilities through selection for appropriate modifier factors. The material from Bat Cave is almost direct evidence in support of this thesis.

The interaction between the various alleles of *Tu* and the introgression of teosinte germplasm is an interesting one which is clearly revealed by some of the cobs in Strata IV and V. In a recent paper (1948) the senior author illustrated a spike of tunicate teosinte produced by introducing the *Tu* gene into teosinte through repeated back-crossing. The rachis was reduced to a slender disarticulating stem. The prominent glumes, quite distinct from the bony glumes of teosinte in size and structure, had, nevertheless, taken on a coriaceous quality very different from the papery or chaffy glumes of pod corn. They seemed almost to be a product of distributing over a large volume of tissue all of the factors for hardness and stiffness ordinarily found in a small volume.

Teosinte introgression has similar effects upon genotypes representing lower alleles in the *Tu-tu* series. Plate XXVI, Figs. F, G, H, illustrates three cobs from Bat Cave which are similar, if not identical, with respect to their alleles of *Tu*, but which differ decidedly in the amount of teosinte introgression.

Evidence for introgression of teosinte germplasm into maize was not confined to a general increase in the hardness of the rachis and outer glumes, since individual characteristics of teosinte also made their appearance. Three cobs were found with the distichous arrangement characteristic of teosinte. These occurred in Strata IV, V, and VI. Two cobs were found which bore single spikelets, also a teosinte characteristic. These occurred in Strata

IV and V. All of the evidence combined points to two conclusions with respect to the rôle of teosinte in the origin and evolution of maize: (1) Maize did not originate from teosinte; (2) The course of evolution of maize in its later stages has been strongly affected by an introgression of teosinte germplasm. If it should ever be established beyond a reasonable doubt that teosinte is a hybrid of maize and Tripsacum, then a third important conclusion would be possible; namely that the hybridization between maize and Tripsacum which produced teosinte must have occurred not later than 500 B.C. and perhaps considerably earlier.

Evolution of Kernel Size

The primitive people who grew the maize whose remains were found in Bat Cave were evidently extremely efficient in their corn-shelling operations. Not a single cob among the 766 recovered from the digging bore even one normal kernel. However, a total of 125 loose kernels, all reasonably well-preserved, were uncovered in the refuse and some of these were found in each of the six layers. The kernels in each of the two lower strata are small and corneous, and were undoubtedly capable of popping. Thus, the primitive maize of Bat Cave was, as Sturtevant (1894) supposed primitive corn to be, both a *pod* corn and a *pop* corn.

The kernels, like the cobs, show a progressive increase in mean size from stratum to stratum. They were measured in three dimensions and, since the calipers used registered in thousandths of an inch, these units were also used in computing the mean as well as the maximum and minimum dimensions which are set forth in Table I.

It is apparent from the data in Table I that, while there is little change in the mean thickness of the kernels from stratum to stratum, there is a noticeable if somewhat

irregular increase in mean length and a marked and progressive increase in average width. Since kernel width has increased proportionately more than length, it furnishes the most useful dimension for detailed study.

Even more striking than the increase in average kernel width is the progressive increase in the maximum width (width of widest kernel) from stratum to stratum. This increase is virtually linear, but the linearity is probably spurious, since it is scarcely to be believed that the several strata represent identical periods of time, or that genetic changes of a given order always produce the same change in absolute dimensions whether acting upon small or large kernels. Furthermore, part of the increase in maximum size is nothing more than a consequence of increasing the size of the sample. This factor, however, does not account for all of the increase in maximum size, since there is a substantial increase from Stratum IV to Stratum VI, although the samples from the two strata are approximately equal in size. Furthermore, the cobs, even though they lack kernels, furnish indirect evidence of a progressive increase from stratum to stratum in the mean and maximum width of the kernel.

Although there is a progressive increase in kernel width from stratum to stratum, the smaller-kerneled types with which the series began did not disappear from the scene when the new types with larger kernels came into existence. What has actually occurred is that there has been an appreciable increase in the range of variation with respect to kernel size. This is illustrated by Plate XXIV, Fig. A.

The marked increase in variation in kernel size in a relatively short period of time provides some indication of the way in which variability accumulates in a man-made environment in which the pressure of natural selection has been reduced or released. Here, perhaps, is the

key to the enormous diversity found in so many species of cultivated plants and domestic animals. Here, too, perhaps, is a clue to the rapidity with which organisms, in nature, can evolve in the face of drastic changes in the environment.

Evolution of the Husks

Although only eight specimens of husks were found in the Bat Cave remains, these differ sufficiently in their characteristics from stratum to stratum to allow some far-reaching inferences to be drawn with respect to the nature of the primitive maize inflorescence and the evolution of husks during domestication.

No specimens of husks were found in the lowest stratum. Only one specimen was found in Stratum II, but this single specimen, although it represents the husk covering of less than half of the ear, has an extremely important story to tell.

The husk appears to be intact with respect to length and reaches a maximum length of 24.5 cm. Four leaf sheaths are included, and the number may tell something of the relative height at which the ear arose. If primitive maize resembled either of the maize relatives, teosinte or Tripsacum, its lateral branches would have had a node number approximately equal to the node number on the primary stalk above the point of origin of the branch. This allows us to infer that the ear was borne at the fifth node below the tassel, but it tells us nothing about the number of nodes which might have occurred below the ear.

All husks have prominent parallel veins widely spaced. There is no anastomosing venation. It is primitive, undifferentiated husks of this type which produce the "striations" on the surface of the kernels in ears which are tightly enclosed in husks (Anderson 1944a). Striated ker-

nels may therefore be regarded as a primitive character.

Perhaps the most important characteristic of this husk is that it shows no evidence of ever having been shaped around an ear. Furthermore, the stem or shank on which it occurs is quite slender, so slender indeed that, of the cobs which occur in Strata I and II, only a cob similar to that illustrated in Plate XXVII could have been borne on it. The husks, as shown in this Plate, are far longer than needed to enclose an ear of this type.

All of these facts combined point to the almost inescapable conclusion that the husks at this stage in the evolution of maize did not enclose the ear. Instead, they were nothing more than an involucre of leaf sheaths, not greatly modified, subtending and surrounding the base of the pistillate inflorescence, but by no means completely enclosing it.

The remaining seven specimens of husks together are not as interesting as the single specimen found in Stratum II. One of the specimens found in Stratum V appears to be intact or almost so and has a maximum length of 10.5 cm. It includes five leaf sheaths, all glabrous and lacking in leaf blades and ligules. The veins are parallel, but are more closely spaced than in the sheaths found in Stratum II. The husks in Stratum V differ from those in Stratum II primarily in their shape, which gives definite evidence of having once enclosed an ear.

Two other specimens found in Stratum V differ from the one described immediately above in having scattered hairs and numerous prickles on the outer sheaths and anastomosing venation on the inner. Both show evidence of having once enclosed an ear.

The four specimens found in Stratum VI are too fragmentary to be of great value. Two of the specimens, however, show evidence of having once been shaped around an ear. Two of the four specimens are glabrous.

The third has its inner surface beset with short prickles while the outer bears scattered hairs and prickles. The last specimen bears numerous short hairs on the inner surface and between the veins on the outer surface. The veins themselves bear longer and more numerous hairs on the outer surface. Only parallel venation was found on three of the four fragments; anastomosing venation was apparent on the fourth.

Cutler (1946) has pointed out that the husks of maize are not fundamentally different from a variety of similar structures found in other genera of grasses, and he compares them specifically with a kind of fasciation sometimes occurring in the genus Trichachne in which the lateral inflorescence is enclosed by the leaves of the culm on which it is borne. The husks found in Stratum II of the Bat Cave remains would indicate that Cutler's comparison is valid. Furthermore, the later evolution of the husk covering is quite consistent with the modification of leaf sheaths which occur in other grasses.

The leaf sheaths which comprise the husks obviously became wider during the evolution of maize and eventually completely enclosed the ear. The leaf blade and ligule were lost. The outer and inner sheaths became differentiated, the latter becoming thin and papery with anastomosing venation and were no longer capable of producing striations on the kernels. These changes are quite in keeping with the morphological pattern in other genera of grasses. Arber (1934), speaking of modification of leaf sheaths in the grasses, makes the following statement:

"An exaggeration of the size [width] of the leaf-sheath, and a corresponding reduction in the limb, occur as part of the normal development in the uppermost foliage leaf enclosing the inflorescence in many grasses, such as *Phalaris canariensis* L. and *Alopecurus pratensis* L. In the xerophytic South African grass, *Ehrharta aphylla* Schrad., this type of change has gone so far that the lamina is reduced to a mere point."[1]

[1] Reference to figures omitted in this quotation.

The figures that accompany Arber's statement are particularly interesting in illustrating the marked broadening of the sheath in *Phalaris canariensis* and the reduction of the leaf blade to a mere point in *Ehrharta*.

Arber also describes and illustrates a broadening and shortening of the leaf sheaths and a reduction in the laminae in *Agropyron repens* Beauv., resulting from injury by insects. And Hitchcock (1935) illustrates a number of species of grasses in which the sheath or sheaths immediately below the inflorescence have become shorter and broader and have largely lost their laminae. It is evident, therefore, that the development of the husks in maize is nothing more than an exaggerated form of a morphological development which is widely distributed in the Gramineae.

In several recent papers (1946, 1948) the senior author described the evolutionary steps which were thought to have occurred in maize during evolution under domestication. In the light of the direct evidence now bearing on this point the views previously expressed are subject to possible modification. For example, it was assumed that wild maize bore mixed staminate and pistillate inflorescences terminally on lateral branches whose sheaths and laminae were essentially identical with those on the main stalk. Although this assumption has not yet been shown to be erroneous, another possibility is now apparent. It is quite possible that wild maize already had distinct staminate and pistillate inflorescences, and that a shortening of the internodes immediately below the pistillate inflorescence had already occurred, giving rise to an involucre of leaf sheaths which surrounded the base of the ear but did not enclose it. There is no reason why a plant with such an inflorescence could not have existed in a wild state. There is, at least, no doubt that such a plant did exist in the early stages of domestication.

One more important and clear-cut conclusion can be drawn from the evidence furnished by the prehistoric husks. Had maize originated from teosinte, as some botanists still suppose, then the early primitive races of maize, only slightly removed from teosinte in their characteristics, might be expected to possess short husks scarcely covering the ears. The early evolution of the husks would then have become a matter of a progressive increase in length to enable the husks to enclose progressively longer ears. In the Bat Cave material the evolutionary sequence in the husks is exactly the reverse of this. The earliest husks are the longest. Indeed, they are several times longer than the longest ear in the same stratum. The early evolution of husks has been a matter of their becoming shorter and wider rather than longer.

Thus, the accumulated circumstantial evidence against the hypothesis that maize originated from teosinte is finally reinforced by direct evidence which is almost conclusive.

Leaf Sheaths

In addition to the husks which are largely modified leaf sheaths, ten specimens of true leaf sheaths were found—one from Stratum IV, the remaining nine from VI. The specimen from Stratum IV is completely glabrous; of the nine specimens from VI, four are completely glabrous on both inner and outer surfaces, three have hairs and prickles on both surfaces, one is glabrous on the outer surface and beset with numerous short hairs on the inner, and one bears short hairs on the outer surface but is glabrous on the inner.

The significance of these variations is not yet clear. Only one fact is certain. At least part of the maize found in Bat Cave possessed glabrous leaf sheaths. True glabrousness is not common in maize varieties today, except

among those grown at high altitudes in Ecuador, Peru and Bolivia, although it is occasionally encountered in Guatemala[1] and Mexico. The inheritance of glabrousness (unpublished data) does not appear to be particularly complex and it is possible that the characteristic has appeared more than once in the evolution of maize under domestication. On the other hand, the fact that there is a large center of glabrous maize at high altitudes in South America may not be without significance in connection with a consideration of the early glabrous maize from Bat Cave which also grew at a relatively high altitude.

Tassels

Anderson and his co-workers (1942, 1944b, 1948) have repeatedly emphasized the importance of studying the maize tassel as a means of understanding the morphology of the ear, and in studying the tassel they have discovered an array of characteristics which promise to be invaluable in the classification of living maize varieties. Tassels, however, are by no means as enduring as ears and cobs, nor are they so likely to be collected in great numbers by primitive peoples or deposited by them in refuse heaps or graves. Only five specimens of tassels were found in the Bat Cave remains, one in Stratum III, three in IV and one in V.

The specimen in Stratum III consisted of a fragment of a lateral tassel branch. This included five nodes, of which three each bore an extra spikelet. This condition, first described by Cutler (1946) and called "multiplication," is common in the maize varieties of South America.

[1] Mangelsdorf and Cameron (1942) described as glabrous many varieties from Guatemala. This is an error in terminology. Most of the varieties described by them as glabrous, although lacking the prominent hairiness so characteristic of high-altitude varieties of Mexico and Central America, are actually hispid.

It is superficially similar to, but actually quite different from, a condition which Anderson (1944b) has designated as "condensation," in which there is a telescoping of internodes to the extent that two or more pairs of spikelets *appear* to arise at the same node. Condensation is common in the maize of Mexico and Central America.

The spikelets on the single specimen from Stratum III had their glumes sparsely covered with prickles.

The three specimens from Stratum IV comprised two fragments and one intact tassel. The first, a fragment of a central spike, had its glumes covered with short hairs and prickles and showed neither condensation nor multiplication. The second, a fragment of a branch, had its glumes sparsely covered with hairs and prickles and showed both multiplication and condensation. It included 12 nodes upon which were borne 37 spikelets, 13 more than should have occurred in the absence of both multiplication and condensation. One of the extra spikelets was the result of multiplication; the others, 6 pairs, were the consequence of condensation. The condensation ratio is, therefore, 1.5.

The intact tassel in this stratum comprised a lax central spike and three branches. Its glumes were covered with hairs and prickles, and the tassel showed neither multiplication nor condensation. It is the kind of tassel, which, among living varieties, is found only in early-maturing types.

The single specimen found in Stratum V had its glumes covered with long hairs. The fragment included 21 nodes and was free of both condensation and multiplication since there were no extra spikelets at any node.

No pistillate spikelets were found in any of the fragments or in the intact tassel.

So far as these few tassel specimens have any bearing upon the problem of evolution in maize, they suggest,

but certainly do not prove, that (1) multiplication preceded condensation in this sequence, and (2) the maize grown by the Bat Cave people was early-maturing.

Primitive Maize Reconstructed

From a study of the cobs found in the lower strata of the Bat Cave material, supplemented by evidence supplied by fragments of husks, sheaths, and tassels, it is now possible to reconstruct a primitive maize with a substantial measure of confidence in the reliability of the reconstruction. The earliest Bat Cave material, which was probably an early-maturing race, had glabrous leaf sheaths. Its tassels bore lax central spikes and were sparsely branched. There was no condensation of the spikelets. Its ear, borne several nodes below the tassel, was surrounded, but not enclosed, by an involucre of slightly modified leaf sheaths (some bearing ligules and rudimentary laminae) which were at least twice as long as the ear itself. The small ear arising from the center of this involucre was a typical grass spike bearing paired pistillate spikelets on a slender rachis. The phyllotaxy was definitely spiral. Indeed, it was so strongly spiral that, in some cases, the cupule from which the spikelets arose was not at right angles to the vertical axis of the rachis but was more or less parallel to the sloping path of the spiral.[1] The lower glumes of the spikelets were fleshy, slightly flattened and lacking in conspicuous venation. They were quite similar to the glumes of sorghum and, like them, they did not completely enclose one half of the kernel. The upper glumes were somewhat longer than were the lower, a condition common among grasses, and were glabrous, chaffy, strongly veined, boat-shaped, and enclosed half of the kernel with length to spare. The

[1] In a previous paper the senior author (1945) expressed the opinion that spiral phyllotaxy in maize is largely the product of introgression from teosinte. He could scarcely have been more wrong.

kernels were small, slightly longer than wide, and corneous. This maize was both a pop corn and a pod corn.

An artist's reconstruction of this primitive maize, executed by Mr. Gordon W. Dillon to whom we are indebted not only for his artistry but also for his botanical acumen, is shown in Plate XXIV, Fig. B. In its phyllotaxy and the nature of its glumes the reconstruction is based upon an actual specimen from Stratum I illustrated in Plate XXIV, Fig. C. Since this specimen was not intact with respect to length, the reconstructed ear was drawn to correspond in length to an intact specimen in the same stratum. The size of the kernels in the reconstruction was determined by the shape of the upper glume which, as shown by examination under the microscope, had obviously partially enclosed a kernel. The kernels on the reconstructed ear are somewhat smaller than any which were actually found in Stratum II, but no smaller than several found in later strata.

It is possible that the kernels in primitive maize were not so completely enclosed by glumes as the artist's reconstruction would suggest and were actually more like kernels of varieties of grain sorghum which, although shorter than their glumes, are large enough to push the lower and upper glumes apart. In all other respects, however, Mr. Dillon's drawing represents an accurate and valid reconstruction of actual remains found in the lowest stratum of the Bat Cave material.

Factors Involved in the Evolution of Maize

The evolutionary steps required to transform the primitive Bat Cave maize into a modern Corn-Belt Dent are no longer difficult to visualize. Indeed, many of them are clearly illustrated by the vegetal remains described in this paper. Elucidation of the remainder requires little more than a judicious use of the imagination.

The three principal factors in the evolution of maize have probably been: (1) a reduction in the pressure of natural selection; (2) a change in the alleles at the *Tu-tu* locus; (3) an introgression of teosinte germplasm into maize.

The principal effect of the first factor has been a tremendous increase in total variation. Variations, which in nature would have been rigidly selected against, survive and accumulate in a man-made environment where the struggle for existence is reduced to intra-specific competition. There is no evidence that human selection was an important factor in the early evolution of maize under domestication. Thus, in the absence of natural selection, and before human selection became a factor, the trend was one of creating a wider and wider range of variation.

The changes in the alleles at the *Tu-tu* locus have already been mentioned, but the full significance of these changes cannot be appreciated without considering the present-day products of this evolutionary trend. It has already been pointed out that changes from the higher to the lower alleles at the *Tu-tu* locus result in a reduction in the size of the glumes and an increase in the size of the rachis. These are the primary effects. The secondary effects, which are perhaps even more important, include a substantial increase in the vascular system of the ear, and a reduction in the length of the rachillae upon which the spikelets are borne. Cutler and Cutler (1948) state that the rachilla in teosinte, and in some species of Tripsacum, is compacted. They state further that in races of maize with long, slender rachillae the grains yield to pressure and can be pushed into the cob, while in races with compact rachillae the grains are firm.

All of these characteristics can easily be studied, with no more equipment than a pair of calipers and a rule, by an examination of the cross section of an ear exposed by

breaking the ear in two. It has already been mentioned that the cross section of a shelled cob comprises two concentric circles, the inner enclosing the zone of rachis tissue, and the outer the zone of glume tissue. The four upper diagrams in Plate XXVIII show cross sections of four cobs from Bat Cave and illustrate a sequence of changes in the cob/rachis index.

When the kernels are still attached to a cob, the cross section comprises three instead of two concentric circles, the diameter of the third circle representing the distance to the dorsal surface of the kernels. In true pod corn (*tuhtuh* and *Tutu* in Plate XXVIII) the third circle may lie within the second, but in all other types of maize it lies without. Now, if the average length of the kernels themselves is ascertained (for example, by measuring ten kernels laid end to end), the point at which the base of the kernels is attached to the rachillae is easily determined by measuring in from the third circle a distance equivalent to the average length of the kernel. These distances are shown by broken lines within the glume zone in the diagrams in Plate XXVIII. All of these are based upon actual diameters of the three concentric circles described above and, although fundamentally simple, are highly significant. They reveal, for example, that in the three genotypes *tuhtuh*, *tuhtu* and *tutu* from a relatively isogenic stock derived by repeated back-crossing to Inbred A158, there is a progressive increase in the diameter of the rachis, a progressive decrease in the size of the glume zone and a progressive shortening of the distance between the surface of the rachis and the base of the kernels. A similar comparison between *Tutu* and *tuhtu*, also in a relatively isogenic stock resulting from back-crossing to Inbred P39, illustrates a similar situation. In both of these series the changing relationship of rachis, glumes and kernels is entirely a matter of alleles at the *Tu-tu*

locus. There is no doubt, however, that in nature teosinte introgression also has had its effects superimposed upon these. One of the most important of these effects is a toughening and hardening of the tissues of the glumes and rachis. Had this not occurred, the massive rachis and the short glumes of modern varieties could scarcely have come into existence.

The diagram of modern Dent corn (Plate XXVIII, fourth row) illustrates the lengths to which the evolutionary trends revealed by the Bat Cave cobs have now gone. The rachis has become massive and capable of enclosing an enormous vascular system. The glume zone has been reduced to a minimum, but the glumes have become more or less indurated. The distance between the surface of the rachis and the base of the kernels has been drastically shortened. The entire ear has become an extremely efficient grain-bearing structure, one which, to be sure, would scarcely be capable of surviving in the wild, but which in a man-made environment has no peer among cultivated cereals. Maize is, in many respects, the most efficient producer of foodstuffs among the cereals, and one of the factors in that efficiency is undoubtedly the nature of its pistillate inflorescence.

The Place of Origin of Maize

The evidence from Bat Cave sheds no new light upon the place of origin of maize as a wild plant. It seems scarcely possible that maize could have existed as a wild plant in the vicinity of Bat Cave since the present and past vegetation of this region is made up largely of xerophytic or near-xerophytic species. Furthermore, there is no more reason for suspecting that maize originated here than for believing that beans and squashes also had their origin in this region.

Mangelsdorf and Reeves (1939) concluded that maize

had its origin as a wild pod corn in the lowlands of South America. The origin of maize from pod corn is well established by the Bat Cave remains, but this does not prove that maize originated in South America. The fact that weak alleles of pod corn still have their highest frequency in South America may be of some significance in this connection. Also significant may be the fact that the earliest Bat Cave maize is glabrous and that there is a center of glabrous maize in the highlands of Bolivia, Peru and Ecuador.

If an exact dating of the Bat Cave remains can be agreed upon, perhaps a correlation of the Bat Cave maize with prehistoric maize of the same period in South America will throw new light on the problem. In the meantime, the question of where maize originated as a wild plant is not answered by the new evidence.

Summary

1. Remains of maize isolated from a cultural deposit in Bat Cave in New Mexico reveal a distinct evolutionary sequence.

2. The remains are conservatively estimated to represent a span of approximately 3000 years, beginning not later than 2500 B.C. They may actually have begun much earlier.

3. The maize excavated from the lower strata is the most primitive maize so far known. It is both a pod corn and a pop corn. The ear is not enclosed in husks, but is surrounded at its base by an involucre of leaf sheaths.

4. This early maize is clearly not derived from teosinte.

5. Beginning about midway in the sequence, there is strong evidence of an introgression of teosinte germplasm into maize.

6. There is a progressive increase in cob and kernel size from stratum to stratum.

7. Since ancient types did not disappear completely when new types came into existence, there is a progressive increase in total variability from stratum to stratum. This factor is believed to be of particular significance in the evolution of cultivated plants in general.

8. Changes in alleles at the *Tu-tu* locus and an introgression of teosinte are believed to be the two most important factors in the evolution of maize. These involve a progressive increase in the size of the rachis and the vascular system of the ear, a reduction in the size of the glumes, a shortening of the distance between the rachis and the base of the kernels and a hardening and stiffening of rachis and glume tissues.

9. The problem of where maize originated as a wild plant is not solved by the new evidence.

Acknowledgments

It would be difficult to acknowledge the full extent of our indebtedness to Mr. Herbert W. Dick, whose capable leadership made possible the success of the 1948 Bat Cave Expedition and whose recognition of the importance of vegetal remains is directly responsible for the archaeological material upon which this paper is based. We are also grateful to Mr. Gordon W. Dillon for his reconstruction of primitive maize and to C. Parker Mangelsdorf for the diagrammatic illustrations of cross sections of various types of ears.

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EXPLANATION OF THE ILLUSTRATIONS

PLATE XXIII. The largest cobs, about two thirds natural size, found in each of the six successive strata in the Bat Cave material. Although there has been a progressive increase in maximum size from stratum to stratum, the type found in the first stratum has persisted throughout the series.

PLATE XXIV. A. Variations in kernel size in the six successive strata of the Bat Cave material, natural size. The kernels, like the cobs, have increased in mean size from stratum to stratum, but the smallest size has persisted throughout the series. B. An artist's reconstruction, natural size, of the primitive pod-pop corn found in the lowest stratum of the Bat Cave refuse heap. This primitive maize shows no evidence of having been derived from teosinte. C. The cob from Stratum I, natural size, upon which the reconstruction in B is based.

PLATE XXV. A. A cob, natural size, with prominent horny glumes produced experimentally from a maize-teosinte hybrid. The cob has been soaked in sulphuric acid to simulate aging. B, C, D, E and F are cobs from the upper strata of the Bat Cave showing teosinte introgression, natural size.

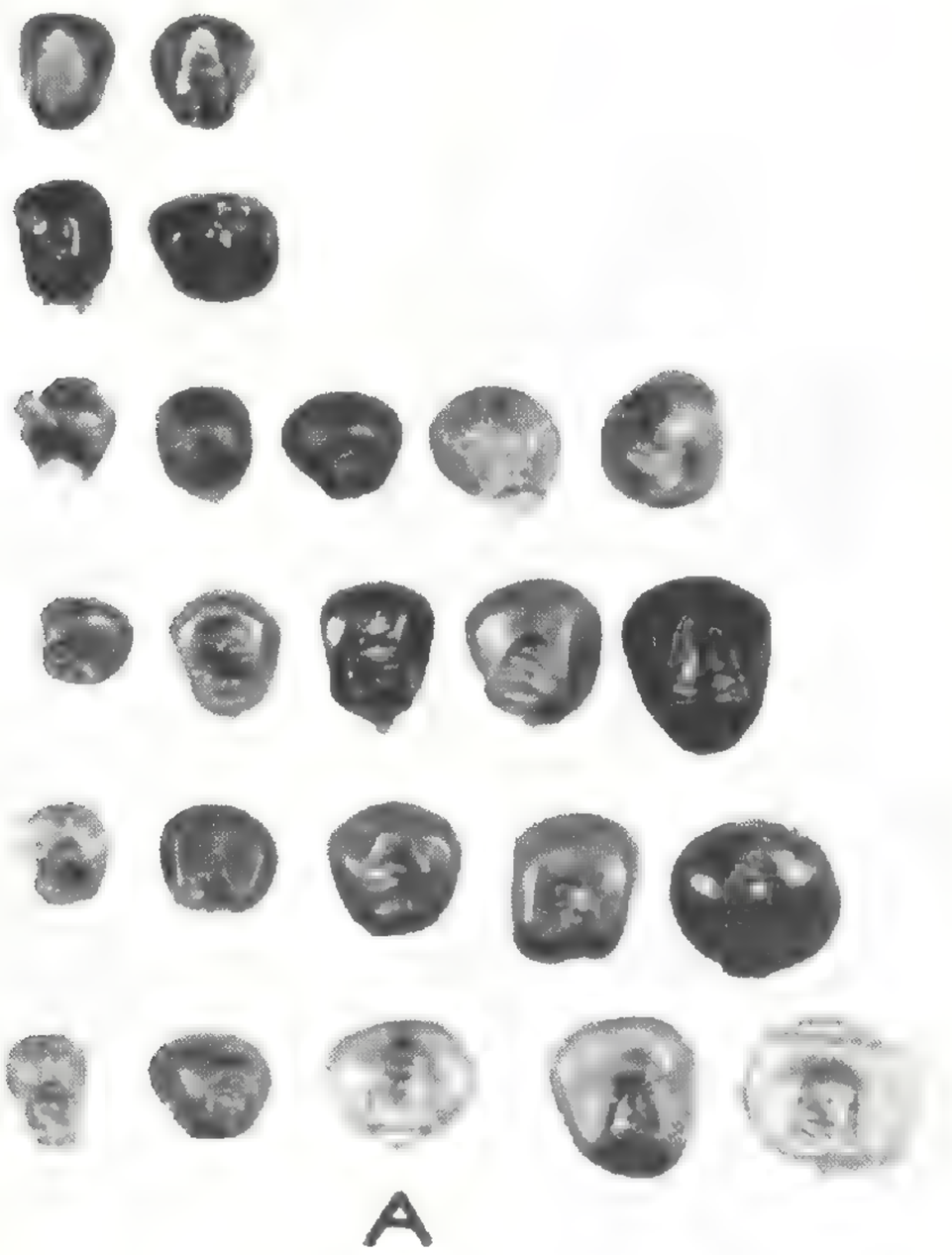
PLATE XXVI. Bat Cave cobs, natural size, showing individual teosinte characteristics. A, B, C. Distichous spikes from Strata IV, V and VI, respectively. D, E. Cobs bearing some single spikelets, from Strata IV and V, respectively. F, G, H. Three cobs which are similar in their *Tu* alleles, but which differ in the degree of teosinte introgression.

PLATE XXVII. A fragment of husk found in Stratum II and the kind of ear which it must once have covered, about two thirds natural size. The husk consists of four leaf sheaths which show no evidence of ever having enclosed an ear. They probably formed an involucre around the base of the ear.

PLATE XXVIII. Diagrams illustrating the cross sections of cobs of Bat Cave maize and ears of modern varieties. *Upper Row.* Four cobs from Bat Cave showing a progressive increase in the size of the rachis accompanied by a progressive increase in the row number and a decrease in the glume zone. *Second Row.* Diagrams of three degrees of half-tunicate in an isogenic stock showing how the lower alleles increase the diameter of the rachis, reduce the glume zone and shorten the distance between the rachis and the base of the kernels. *Third Row.* Diagrams of two degrees of tunicate in an isogenic stock illustrating the same phenomena described above. *Fourth Row.* Three ears of modern maize illustrating various stages in the evolutionary trend toward a massive rachis, short glumes and compact rachillae.

Plate XXIII

Plate XXIV



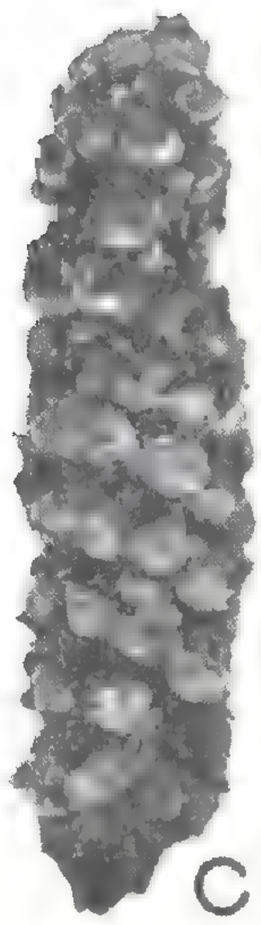


Plate XXV

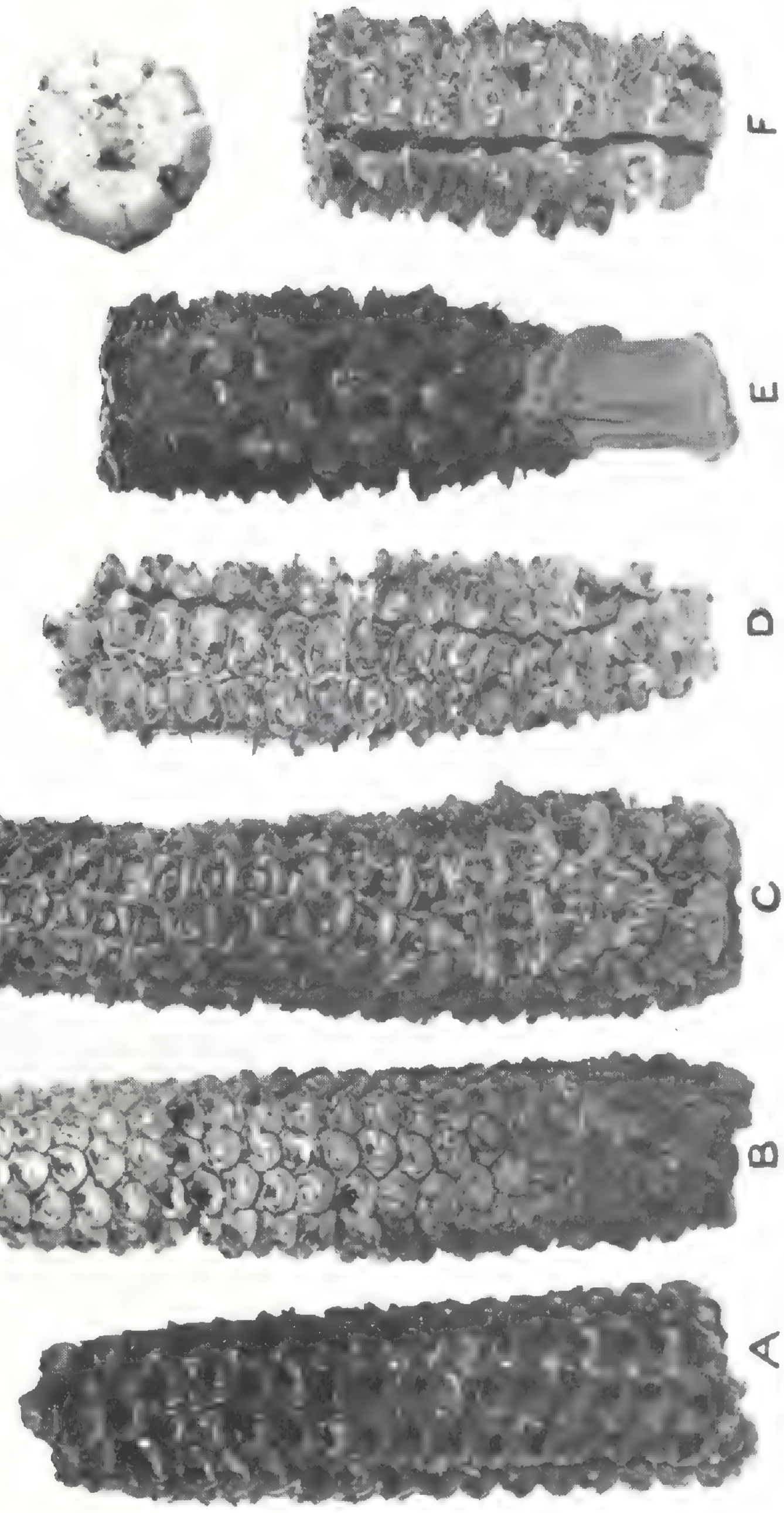


Plate XXVI

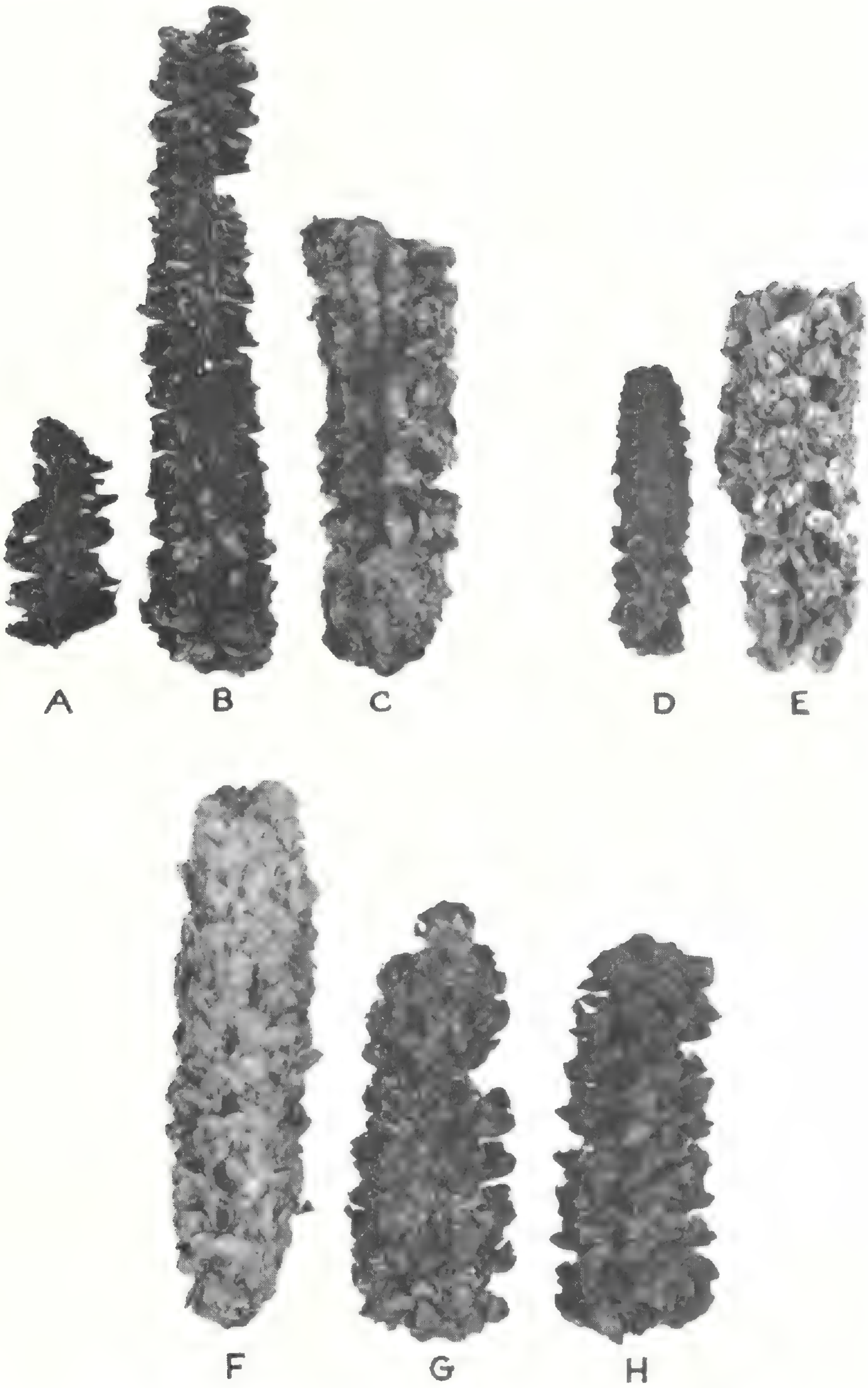
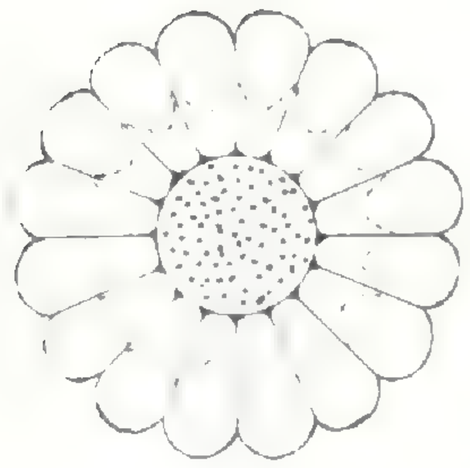


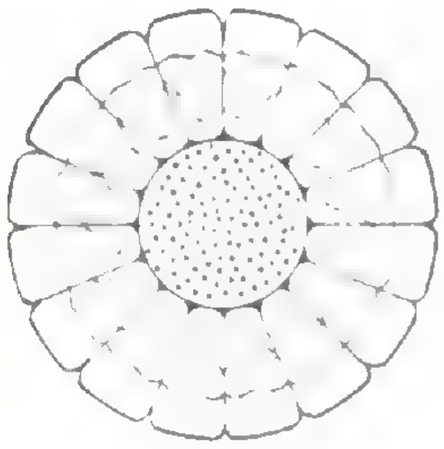
Plate XXVII

Plate XXVIII

PREHISTORIC COBS FROM BAT-CAVE



tu^h tu^h



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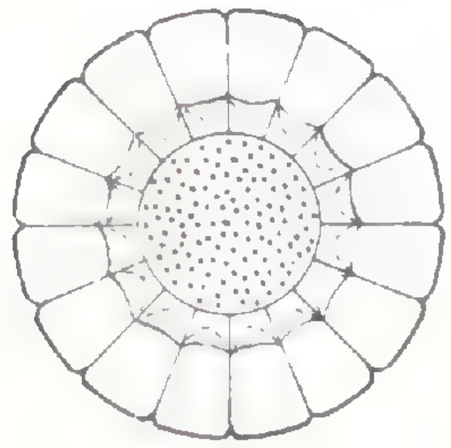

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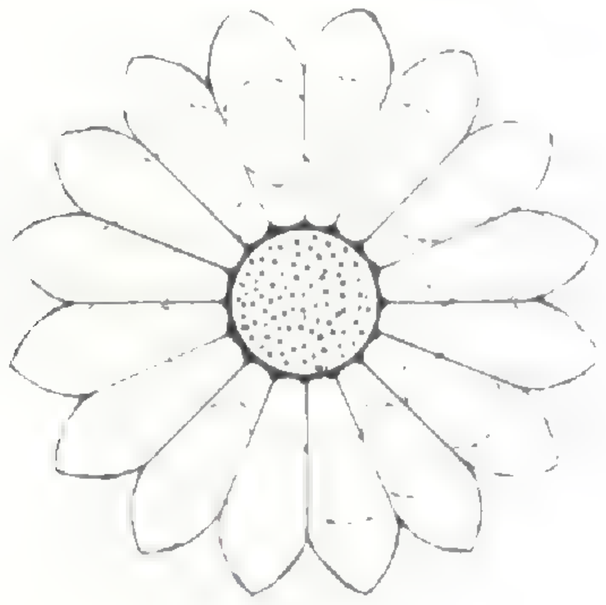

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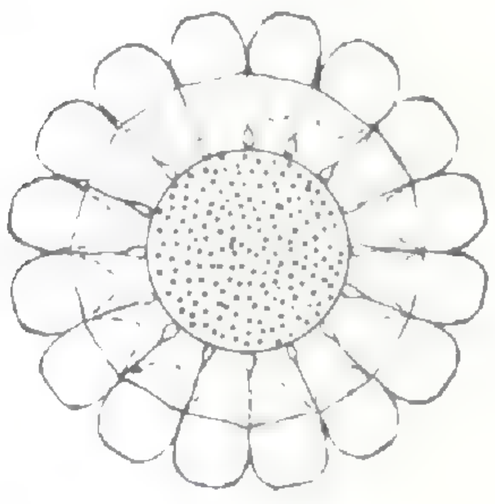
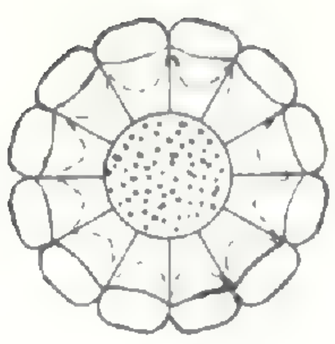
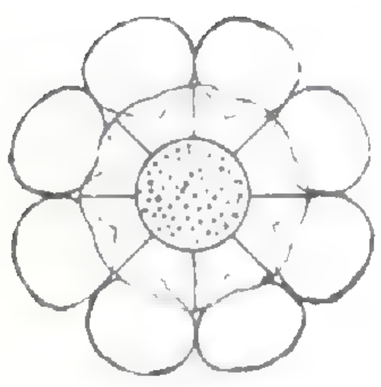


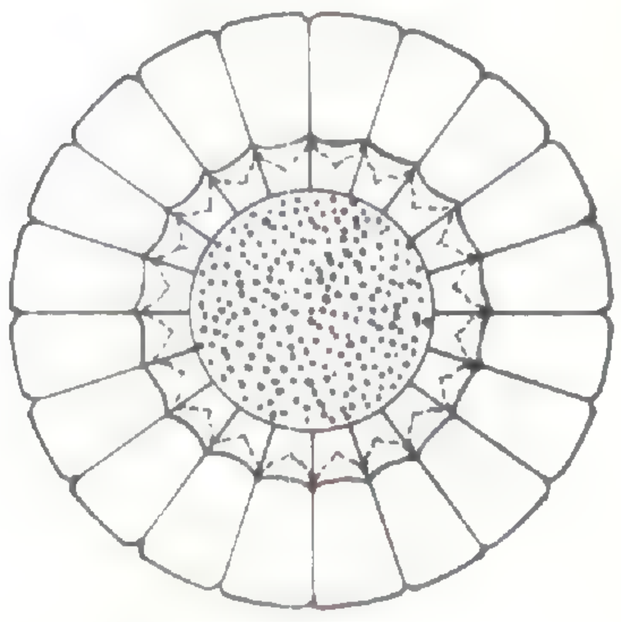
tu^h tu



CHAPALOTE



HIDATSA



MODERN DENT

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, APRIL 18, 1949 VOL. 13, NO. 9

PLANTAE AUSTRO-AMERICANAE V
DE PLANTIS PRINCIPALITER COLOMBIAE OBSERVATIONES

BY

RICHARD EVANS SCHULTES

A NUMBER of recently made collections, chiefly from Amazonian Colombia, represent hitherto undescribed concepts or range extensions or are the basis of interesting ethnobotanical observations. It appears advisable to present the following miscellany of notes on the significance of these collections as a contribution to our understanding of the South American flora, especially that of the northwesternmost reaches of the Amazonian system.

It is with pleasure that I thank Dr. B. A. Krukoff and Mr. Joseph Monachino of the New York Botanical Garden for determining the collections of *Menispermaceae* and *Strychnos;* Mr. Charles Schweinfurth of the Botanical Museum of Harvard University for identifying the orchids; and Dr. Adolpho Ducke of the Instituto Agronômico do Norte (Belém do Pará) for naming the collection of *Leptothyrsa Sprucei.*

ORCHIDACEAE

Cattleya violacea (*HBK.*) *Rolfe* in Gard. Chron. ser. 3, 5 (1889) 802.

Cattleya violacea is well known from Amazonian Brazil, from southern Venezuela and British Guiana. In

Colombia, it has previously been collected (*Haught 2810*) at San José de Ocune on the Río Vichada, to the northeast of the locality of *Schultes 5380*.

Colombia: Comisaría del Vaupés, Macaya-Ajaju River confluence: Mount Chiribiquete. Quartzite base. Summit 800–1200 ft. above forest floor, 1700–2100 ft. above sea level. "Epiphyte. Sepals deep violet, lip deep purple. Spicy fragrance." May 15–16, 1943, *Richard Evans Schultes 5380*.

Pleurothallis ciliata *Knowles & Westcott* Flor. Cab. 1 (1837) 39.

This interesting little orchid has hitherto not been recorded from Colombia. It is known from Trinidad, British Guiana and Peru.

Colombia: Comisaría del Vaupés, Macaya-Ajaju River confluence: Mount Chiribiquete. Quartzite base. Summit 800–1200 ft. above forest floor, 1700–2100 ft. above sea level. "Epiphytic on *Hevea* in forest. All parts of flower yellow." May 15–16, 1943, *Richard Evans Schultes 5418*.

Sobralia rosea *Poeppig & Endlicher* Nov. Gen. ac Sp. 1 (1836) 54, t. 93.

Known from the eastern Andean slopes of Ecuador and Peru, *Sobralia rosea* has previously been reported from Colombia on the basis of a collection from Norte de Santander (Schlechter in Fedde Repert. Beihefte 7 (1920) 212). The locality of *Schultes & Smith 3049*, though very distant from the only other Colombian collection, fills in an extensive gap in our knowledge of the range of this beautiful orchid.

Colombia: Comisaría del Putumayo, Cerro de Portachuelo, entre Mocoa y Sacchamates, alt. ca. 1600–2000 m. "Large clumps with erect stems 8–12 ft. tall. Flowers white; lip fringed with purple." December 9, 1942, *Richard Evans Schultes & C. Earle Smith 3049*.—Comisaría del Putumayo, Río San Miguel ó Sucumbios, Santa Rosa y los alrededores; alt. 380 m.? "Flowers white, tips of column purple." April 7–8, 1942, *Richard Evans Schultes 3559*.

Vellozia phantasmagoria *R. E. Schultes* in Bot. Mus. Leafl. Harvard Univ. 12 (1946) 130, t. XIX, XX.

The sterile collection cited below establishes the occurrence of the curious *Vellozia phantasmagoria* far to the west of its hitherto known range. It was found by Schultes on Cerro Chiribiquete (its type locality) in the upper Río Apaporis drainage-area; and by Paul H. Allen on Cerro Yapobodá, not far from Mitú, in the lower course of the Colombian Vaupés.

COLOMBIA: Comisaría del Vaupés, Río Nequiení (affluent of Río Guainía), Cerro Monachi "Hanging on rocky crags." June 1948, *Richard Evans Schultes & Francisco López 10067*.

MENISPERMACEAE

Abuta grandifolia (*Mart.*) *Sandwith* in Kew Bull. (1937) 397.

Abuta grandifolia, widespread throughout the Amazon Valley and adjacent areas of northern South America, has previously been known from the Vaupés, Caquetá and Putumayo drainage-areas of Colombia (Krukoff and Moldenke in Brittonia 3 (1938) 60; in Bull. Torrey Bot. Club 68 (1941) 240). The Siona Indians of the Putumayo utilize an infusion of the leaves of this plant in treating fevers.

COLOMBIA: Intendencia del Amazonas, Río Putumayo, carretera entre Caucaya (Puerto Leguízamo) y La Tagua, alt. 225 m. "Small tree." May 17, 1942, *Richard Evans Schultes 3740*.

Abuta splendida *Krukoff & Moldenke* in Bull. Torrey Bot. Club 68 (1941) 241.

Described from Bolivian material, *Abuta splendida* has not hitherto been known from the Colombian flora.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Nonejo y los alrededores, frente a la Quebrada Conejo. Nombre kofán: *sa-pé-pa*. 2–5 abril, 1942, *Richard Evans Schultes 3525*.

Chondodendron toxicoferum (*Wedd.*) *Krukoff & Moldenke* in Brittonia 3 (1939) 338.

This species is well known as an ingredient of arrow-poison in the Amazon Region. Known from Amazonian Peru and Brazil (as *Chondodendron polyanthum*), it was first collected by Castlenau at Pebas in Loreto, Peru, where the Yaguas Indians were utilizing it in the manufacture of curare (Krukoff and Moldenke in Brittonia 3 (1938) 22–23, 338). It has hitherto been collected in Colombia apparently only once: the collection *W. Foa 12b*, which states "poison used for blowpipes," is labelled as coming from "Entre Ríos," a now non-existent settlement on the Río Karaparaná in the Intendencia del Amazonas in Witoto Indian country.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Conejo y los alrededores, frente a la Quebrada Conejo. Nombre kofán: *sa-pé-pa*. "Wood of stem crushed to make curare poison." 2–5 abril, 1942, *Richard Evans Schultes 3522*.—Comisaría del Amazonas, Rio Hamacayacu. Common name: *quina*. [April] 1943, *F. J. Hermann 11309*.

BALANOPHORACEAE

Helosis guyannensis *L. C. Richard* in Mém. Mus. Hist. Nat. Paris 8 (1822) 416, t. 20.

This is the second collection of *Helosis guyannensis* known from Amazonian Colombia. The first was reported by Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1946) 117.

COLOMBIA: Intendencia del Amazonas, Río Boiauassú. "Mata virgem. Parásita. Toda a planta e encarnada clara." Ocotober 29, 1946, *George A. Black & Richard Evans Schultes 46–241*.

NYMPHAEACEAE

Victoria regia *Lindley* Monogr. Vict. regia (1837) 3.

Occurring naturally in Colombia probably only along the bank of the Río Amazonas in the trapécio amazónico,

where indeed it is very common and abundant within easy walking distance from Leticia, the magnificent *Victoria regia* has hitherto apparently never been collected in Colombian territory. It has been imported from Brazil and is established in a small pond at La Chorrera on the upper Río Igaraparaná, an affluent of the Río Putumayo.

It is interesting to note that the Spanish-speaking inhabitants of the trapécio amazónico know *Victoria regia* as *horno*, just as in Brazil it is called *forno*. The enormous, flat, round leaves resemble the flat, round baked-clay plates or *hornos* on which fariña is toasted and cassabe is baked; this is the explanation of the curious common name.

COLOMBIA: Intendencia del Amazonas, La Chorrera, Río Igaraparaná. "Cultivated." June 1942, *Richard Evans Schultes 3970A.*—Intendencia del Amazonas, Trapécio amazónico, near mouth of Río Boiauassú, in swampy inlet of Río Amazonas on Isla Zancudo, alt. about 100 m. "Leaves spiny beneath, 4–5 feet across. Flowers large, white, turning red or purplish. *Horno.*" October 1945, *Richard Evans Schultes 6786.*—Intendencia del Amazonas, Trapécio amazónico, Leticia. "Beira do rio em terreno enxarcado, dentro da agua." August 19, 1946, *George A. Black & Richard Evans Schultes 46–18.*

RUTACEAE

Leptothyrsa Sprucei *Hooker filius* in Bentham & Hooker filius Gen. Pl. 1 (1862) 284.

This rare species, described from material collected by Spruce on the Rio Uaupés of Brazil, has apparently never been recorded from Colombia.

COLOMBIA: Intendencia del Amazonas, [Trapécio amazónico]. "Picada Cotuhé, varial aberto, beira de um corrego. Arbusto, 2 m.; flor branca." November 8, 1946, *George A. Black & Richard Evans Schultes 46–364.*

EUPHORBIACEAE

Cunuria crassipes *Mueller-Argoviensis* in Martius Fl. Bras. 11, pt. 2 (1874) 510.

Cunuria crassipes was first collected in Colombia by Allen in 1943 (Baldwin and Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1947) 336). His collection was made on the Río Papurí which forms part of the boundary between Brazil and Colombia. Later, *Cunuria crassipes* was found in the adjacent Brazilian area of the upper Rio Negro and some of its affluents by Baldwin and by Fróes (Baldwin and Schultes, loc. cit.), never at any great distance from the type locality. For this reason, the species was considered to represent a rather restricted endemic.

The most significant collections made recently in the Colombian trapécio amazónico are *Schultes 6909* and *Black & Schultes 46 371*, for they establish the presence of *Cunuria crassipes* very far to the south of the area hitherto considered to be the exclusive home of the species. In 1945, *Schultes 6909*, with several opened capsules but no seeds, was collected during a preliminary study of a low caatinga-like or savanna area on the rather high divide between the Ríos Hamacayacu (Amazon affluent) and Cotuhé (Putumayo affluent). The next year, Mr. George A. Black of the Instituto Agronômico do Norte visited this locality and made the collection *Black & Schultes 46 371*. This collection was sterile, but the large, unusually broad-ovate shape, the relatively thin-papyraceous texture, and the lack of a waxy or glaucescent condition of the upper surface of the leaves all suggested that it might represent a distinct form of *Cunuria crassipes*. The isolation of this station from the nearest known locality of the species seemed to increase the possibility that these differences might be of significance. Accordingly, in September 1948, I sent my assistant, Señor Francisco López, thoroughly familiar with *Cunuria*, to collect more material from the same locality. *López 4* and *5* correspond in every detail with *Schultes 6909* and *Black & Schultes 46 371* and are indeed slightly different

from the abundant material gathered from the upper Rio Negro drainage-area. According to López, the tree is unusually abundant at the locality cited.

Further collections of *Cunuria crassipes* have been made recently in the Río Guainía area in Colombian territory, where the species is represented in unbelievable abundance in the sandy, light-forested caatingas where it is known by the Kuripaka Indian name *á-hoon-da*.

In July 1948, López and I crossed from the Rio Uaupés to the Río Caquetá by way of the Tikié—Ira-Igarapé and the Taraíra—Apaporis. We fully expected to find *Cunuria crassipes* in Colombian territory along the Taraíra, but the species was not seen on the river; in fact, it was not seen south of the headwaters of the Ira-Igarapé, an affluent of the Rio Negro drainage area.

I had never succeeded in finding *Cunuria crassipes* in the region of La Pedrera, although there are abundant areas there where the species might be expected to occur. In November 1948, I was fortunate in being able to accompany General Julio Londoño, of the Colombian army, on a special military flight over the Amazonia of Colombia. In flying extremely low over the La Pedrera region, I saw, in a low-forested caatinga a few miles south of the beginning of the constriction of the Caquetá below the rapids at Córdova (Cupatí), what had all the appearances of numerous small trees of *Cunuria crassipes*. We cannot definitely assert that *Cunuria crassipes* occurs at this point on the Caquetá until actual collections are made, but we may say that it is highly probable that it is represented there.

Colombia: Comisaría del Vaupés, Río Papurí, vicinity of Piracuara Mission, alt. about 200 m. "Trees tall, slightly buttressed, averaging 30 m. in height and 60 cm. in diameter. Bark thin, averaging less than 1 cm. Latex yellowish, scant, coagulating to a non-elastic gum. Flowers greenish yellow. Trispermate *Hevea*-like capsule. Known locally as *wah-so-né-né* in Tukano." August 18, 1943, *Paul H. Allen*

3068.—Comisaría del Amazonas, Trapécio amazónico. Interior regions of trapécio between Amazon and Putumayo water-sheds. Alt. above 100 m. "Tree 50 ft. Spreading crown. Fruit like *Hevea*. Latex white." November 1945, *Richard Evans Schultes 6909*.—Comisaría del Amazonas, Trapécio amazónico, Río Hamacayacu, Quebrada Agua Negra. "Arvore 20 m. Latex branco." November 8, 1946, *George A. Black & Richard Evans Schultes 46–471* (Herb. Inst. Agron. Norte 20477).—Comisaría del Amazonas, Río Hamacayacu, Varial at headwaters of Quebrada Agua Negra. "Small-crowned tree 50 ft. tall. Latex white. Buttress roots slender, low. Bark shaggy, externally dark brown, internally reddish." September 1948, *Francisco López 4*.—Comisaría del Amazonas, Río Hamacayacu, Varial at headwaters of Quebrada Agua Negra. "Buttressed tree 50 ft. tall; diameter of columnar trunk 15 inches. Latex rather thick, white. Bark dark brown." September 1948, *Francisco López 5*.—Comisaría del Vaupés, Río Guainía, region near Sejál. "Slightly buttressed tree 45–50 ft. tall. Bark shaggy, dark brown. Latex thick, white. Wood white." June 1948, *Richard Evans Schultes & Francisco López 10043*.—Comisaría del Vaupés, same locality. "Tree 60 ft. tall with sparse crown. Bark shaggy, dark brown outside, pinkish inside. Fruits rose-red. Latex very thick and white. Leaves very coriaceous." June 1948, *Richard Evans Schultes & Francisco López 10058*.—Comisaría del Vaupés, Rio Naquieni (affluent of Río Guainía), at base of Cerro Monachi. "Tree 40 ft. tall with small buttress roots. Bark thin, brown, roughish. Latex thick, white. Leaves unusually ovate." June 1948, *Richard Evans Schultes & Francisco López 10088*.—Comisaría del Vaupés, same locality. "Tree 50 ft. tall. Buttress roots. Trunk columnar, diameter 14–15 inches. Latex white, thick. Bark dark brown, rough." June 1948, *Richard Evans Schultes & Francisco López 10113*.—Comisaría del Vaupés, same locality. "Tree 45 ft. tall with sparse crown. Latex white." June 1948, *Richard Evans Schultes & Francisco López 10121*.—Comisaría del Vaupés, Río Guainía, Caño Nani below San Antonio. In extensive caatinga. "Tree 50 ft. tall with buttress roots and columnar trunk. Bark shaggy, dark brown outside, light red inside. Latex white. Flowers yellowish." June 1948, *Richard Evans Schultes & Francisco López 10131*.—Comisaría del Vaupés, same locality. In extensive savannah-like caatinga. "Bushy tree, 20 ft. tall with very small buttress roots. Bark dark brown, rough. Latex very thick, white. Leaves unusually round." June 1948, *Richard Evans Schultes & Francisco López 10158*.

Cunuria Spruceana *Baillon* in Adansonia 4 (1863–64) 288.

Cunuria Spruceana was first collected in Colombia by

Allen in 1943, along the Río Papurí, an affluent of the Río Vaupés; in the following year, I collected it from La Pedrera on the Río Caquetá and on the Río Miritiparaná (Baldwin and Schultes loc. cit. 342; Schultes in Caldasia 3 (1945) 247–249). In 1948, more material was collected from La Pedrera.

A most important discovery, however, is that of López who, in September 1948, collected *Cunuria Spruceana* from the headwaters of the Río Hamacayacu, an affluent of the Amazon above Leticia. Later, López and I located a number of trees of this species in the immediate environs of the town of Leticia. Known from a locality in adjacent Peru and from points on the Içá and at São Paulo de Olivença on the Amazonas itself, *Cunuria Spruceana* was to be expected near Leticia, even though several years of intensive collecting had previously failed to disclose its presence there. In the trapécio amazónico, this species occurs sporadically, not in abundance as often is the case in other areas. *Cunuria Spruceana* has no distinctive common name in the Spanish, Portuguese or Tikuna languages in the Leticia area, so far as we could learn.

COLOMBIA: Comisaría del Vaupés, Río Papurí, vicinity of Santa Teresita. "Tall trees averaging 35 m. in height, and 80 cm. in diameter above the conspicuously developed and unique stilt buttresses which are produced to a height of 3–4 m. as laterally compressed board-like flanges which act as flying buttresses, the bases widely detached from the trunk, the arch often high enough for a man to walk upright beneath. Leaves simple, with two basal disk-like glands. Inflorescence of small green flowers from axillary growth. Large trispermate capsule typical of *Hevea*. Bark very thin, 6–8 mm., with scanty latex which coagulates with difficulty, producing a non-elastic gum. Seeds collected by the local Indians for food. Known as *wah-puh* (Tukano)." August 15, 1943, *Paul H. Allen 3063*.—Comisaría del Amazonas, Río Hamacayacu. "Tree 80 ft. tall with huge buttress roots. Flowers yellowish. Latex very thin, white. Bark hard, brownish, thin. Wood white." September 1948, *Francisco López 1*.—Comisaría del Amazonas, Río Hamacayacu. "Tree 60 ft. tall with large buttress roots.

Flowers yellow. Latex white, watery. Bark thin and brittle.'' September 1948, *Francisco López 2.*—Comisaría del Amazonas, Leticia. ''Large tree with large buttress roots. Trunk columnar above buttress roots. Flowers yellowish. Latex watery, white.'' September 1948, *Francisco López 3.*—Comisaría del Vaupés, Río Guainía, near Sejál. ''Enormous tree, 80 ft. tall with large flaring buttress roots. Latex thin, white. Bark thin, hard, dark tan, smooth. Buds yellowish.'' June 1948, *Richard Evans Schultes & Francisco López 10057.*—Comisaría del Vaupés, Río Guainía, at base of Cerro Monachi. ''Enormous tree 85 ft. tall with extensive buttress roots. Latex white, thin.'' June 1948, *Richard Evans Schultes & Francisco López 10135.*—Comisaría del Vaupés, Río Guainía, Caño Nani below San Antonio. ''Buttressed tree 75 ft. tall. Trunk columnar, diameter 18–20 inches. Latex watery, white, sparse.'' June 1948, *Richard Evans Schultes & Francisco López 10163.*—Comisaría del Caquetá, Río Caquetá, La Pedrera, at Angostura. ''Tree 80 ft. tall; huge buttresses; trunk columnar, 2 ft. diameter above buttresses. Bark hard, reddish brown. Latex very thin, white, not coagulating. Flowers yellow.'' July 16, 1948. *Richard Evans Schultes & Francisco López 10221.*—Comisaría del Caquetá, Río Caquetá, La Pedrera, at Angostura. ''Corpulent tree 55 ft. tall, diameter above buttresses 15 inches. Bark hard, thin, reddish brown. Latex thin, watery, white, not coagulating. Flowers yellow.'' July 16, 1948, *Richard Evans Schultes & Francisco López 10222.*—Comisaría del Amazonas, Leticia. ''Corpulent tree 75 ft. tall. Extensive buttress roots up to 6 ft. high. Bark dark brownish-tan, thin, hard. Flowers yellow.'' November 1948, *Richard Evans Schultes & Francisco López 10257.*

Senefeldera chiribiquetensis *R. E. Schultes & L. Croizat* in Caldasia 3 (1944) 122.

Matching the type and topotype material of *Senefeldera chiribiquetensis* perfectly, *Cuatrecasas 7682* establishes the occurrence of this curious endemic slightly northwestward of the type locality which is the confluence of the Ríos Macaya and Ajaju in the Apaporis drainage-area. More interesting, however, is the discovery, through *Cuatrecasas 7684*, that *Senefeldera chiribiquetensis*, hitherto believed to be confined to cretaceous quartzite hills, also occurs on granite of a much earlier (probably Cambrian) age.

A search for *Senefeldera chiribiquetensis* on a number

of granitic peaks in the upper Rio Negro and lower Rio Uaupés in Brazil (of the same age as the granite at San José del Guaviare) has indicated that it is apparently not present on Serra Curicuriarí, Serra Cocuí and similar mountains of the area. Indeed, during my explorations in the upper Rio Negro basin in 1947–48, I found no species of *Senefeldera* whatsoever.

COLOMBIA: "Río Guaviare, San José del Guaviare. Terrenos graníticos, sabana, 270 m. alt. Arbol latex." 12 septiembre, 1939, *J. Cuatrecasas 7682* (U. S. Nat. Herb. 1774175).

HIPPOCRATEACEAE

Tontelea attenuata *Miers* in Trans. Linn. Soc. London Bot. 28 (1872) 384.

According to A.C.Smith (in Brittonia 3 (1940) 474), this beautiful, low tree is known from the original Spruce collections in the Rio Negro country of Brazil, from the basin of the Rio Madeira of Brazil, and from British Guiana and eastern Peru and Colombia. *Schultes 5385* represents the second collection from Colombia. The first was *Klug 1967* from the Putumayo, a great distance from the Vaupés locality cited below.

COLOMBIA: Comisaría del Vaupés, Macaya–Ajaju River confluence, Mount Chiribiquete. Quartzite base. Summit 800–1200 ft. above forest floor, 1700–2100 ft. above sea level. "Small tree. Flowers white, probably turning brown. Odour of cinnamon pronounced. Bark smooth, brown. Along banks." May 15–16, 1943, *Richard Evans Schultes 5385*.

SAPINDACEAE

Paullinia scaberula *R. E. Schultes sp. nov.*

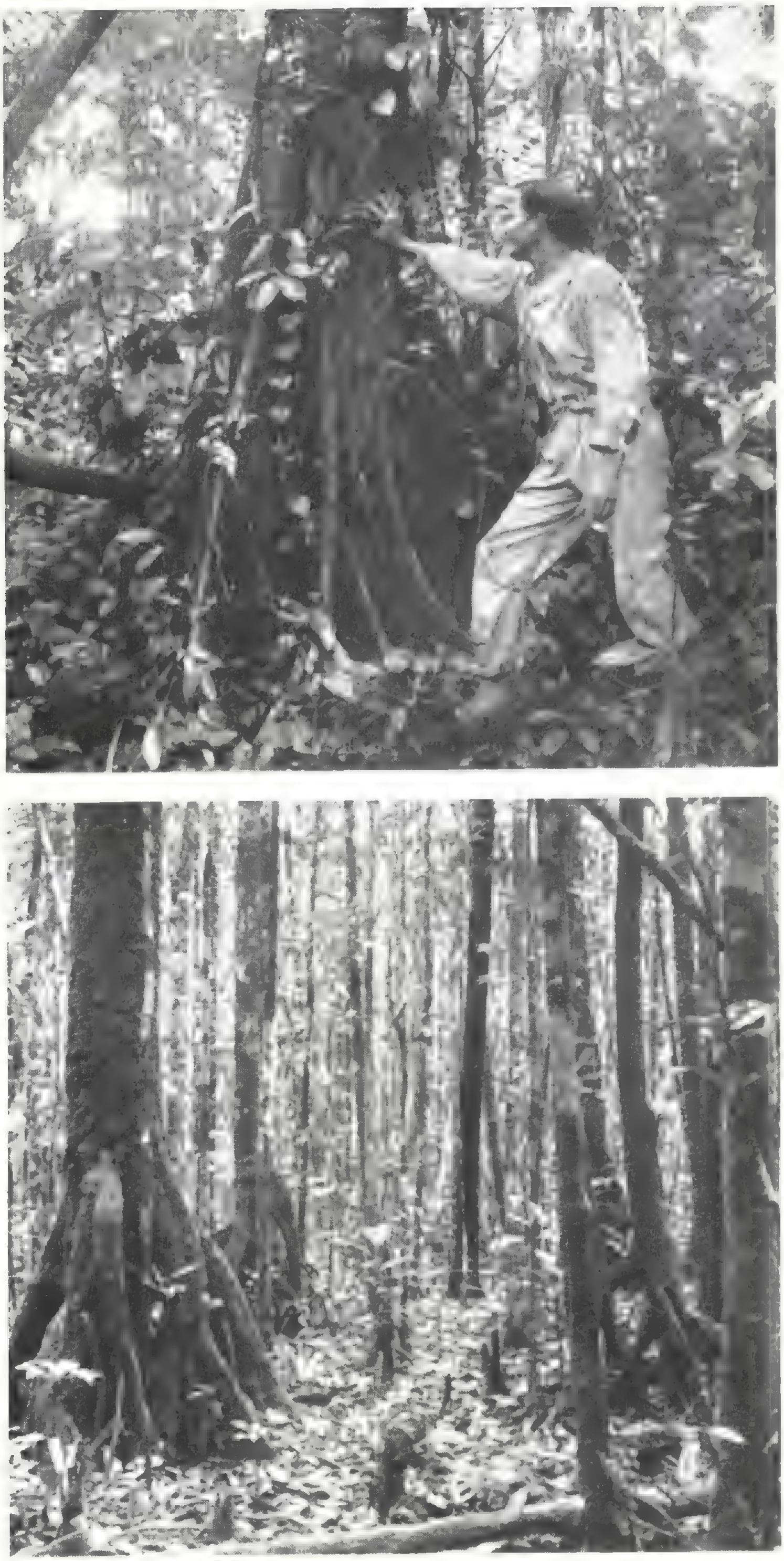
Vitis parva. Rami graciles, fusco-rufo cum cortice et pilis nigris debilibus usque ad 6 mm. longis et dense saetigeribus armati. Ramuli subteretes, similes. Folia quinquepinnata, usque ad 30–35 cm. longa, 25 cm. lata. Rhachis nuda (exalata), firma, scaberula nigris cum pilis,

EXPLANATION OF THE ILLUSTRATIONS

PLATE XXIX. (Upper figure). Basal portion of the trunk of *Septotheca Tessmannii*, the individual from which the collection *Schultes & Black 8612* was made.

(Lower figure). View in a caatinga forest on the Río Naquieni, Comisaría del Vaupés, Colombia. The trees with stilt roots are *Cunuria crassipes;* the slender, columnar trunks represent *Hevea rigidifolia*.

Plate XXIX



plerumque 16 cm. longa, 2 mm. in diametro. Foliola elliptica, 10–15 cm. longa, 5.5–7.5 cm. lata; superiora aequalia, apice acuminata, margine longe et leviter sinuata, valde membranacea, utrinque aspero-pilosa, atroviridia, lateralibus cum nervis plerumque duodecim supra et subtus elevatis, nervis praecipuis et secundariis utrinque pilosis; petioli nudi. Inflorescentiae axillares, racemiformes, multiflorae, 6–8 cm. longae. Pedicelli robusti, 2–4 mm. longi, bracteis minutissimis, triangulari-subulatis, 0.5 mm. longis. Flores parvi, albi. Sepala quinque; duo exteriora crassa, extus et intus glabra, subovalia, apice rotundata, margine ciliata, 1.5 mm. longa, 1.3 mm. lata; tria interiora majora, membranacea, rotundata, intus et extus glabra, fere 2.5 mm. longa, 2 mm. lata, valde inflexa, margine ciliata. Tori glandulosi quattuor, crassi, linguiformes. Petala quattuor, submembranacea, integra, obovata, apice rotundata, glabra, 3–3.5 mm. longa, 1.5 mm. lata. Stamina octo, ex floribus prominenter exserta. Staminum filamenta pilis longioribus lanatisque dense vestita, 1.5–2 mm. longa. Antherae glabrae, 0.4 mm. longae. Ovarium obovoideum, 1 mm. in diametro, glabrum, cum stylo glabro 1 mm. longo coronatum. Stigma profundissime trifidum, lobis crassis, pustulatis et circinnatis. Fructus capsularis, trivalvis, subdrupaceus; capsula oblique ovoidea, in stipitem attenuata, rostrata (styli reliquiis coronata), ecostata et exalata, epicarpio parum crasso, praeter stipitis basim glabra, 6–7 mm. longa, 3–4 mm. lata, rostra usque ad 2 mm. longa.

This new species is unusual in aspect and is distinguished easily by its having black scaberulent hairs along the branchlets.

Brazil: Estado do Amazonas, Sao Paulo de Olivença. "Mata da terra firme. Cipozinho fino, caulifloro, flôr branca." April 3, 1944, *A. Ducke 1628* (Type in Herb. Inst. Agron. Norte, Belém).

Septotheca Tessmannii *Ulbrich* in Notizbl. Bot. Gart. Berlin 9 (1924) 129, t. 3.

This gigantic, upper Amazonian tree, very rare indeed in collections, has hitherto only been observed, never collected, in Colombian territory (Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1946) 118). The two collections cited below establish beyond any doubt that this concept, described from material from the Río Ucayali in Loreto, Peru, and found by Ducke and by Schultes near Tabatinga, Amazonas, Brazil, a few miles from Leticia (Ducke in Bol. Téen. Inst. Agron. Norte 4 (1945) 21–22), is a prominent element of the vegetation of certain areas of the Amazon band of the Colombian *trapécio amazónico* and must be added to our enumeration of Colombian plants.

In November 1948, I returned to the locality of these two collections and discovered that the colony of trees from which they were gathered no longer exists. The current of the Amazon at this point has recently wrought such destruction by washing away several hundred feet of bank that the mouth of the Boiauassú has a different configuration than formerly. (Plate XXIX, upper fig.)

COLOMBIA: Intendencia del Amazonas, Trapécio amazónico, mouth of the Río Boiauassú, alt. about 100 m. "Enormous tree; buttress roots. Flowers yellowish green, mucilaginous. *Sapotilla.*" October 1945, *Richard Evans Schultes 6888.*—Same locality. "Sepals green-yellow. Tree 80 ft. tall, great buttress roots. *Zapoterana.*" October 27, 1946, *Richard Evans Schultes & George A. Black 8612.*

STERCULIACEAE

Herrania albiflora *Goudot* in Ann. Sci. Nat. sér. 3, 2 (1844) 230, t. 5, figs. 1–10.

The specimen cited below, one of the earliest collections of the species, was identified as *Herrania albiflora*

at Kew by Planchon, who annotated the sheet. It is a topotype.

The report of the collector of this specimen relative to his having seen "several hundreds of fruits" on a cultivated tree of *Herrania albiflora* must be recognized as an exaggeration. Although fruits are often very numerous in most species of *Herrania*, I have never met, in my field studies of the genus, any condition which would indicate "hundreds of fruits."

COLOMBIA: Departamento de Cundinamarca, "Río Guaco, near Muzo. *Cacao simaròn* vg. name, in some districts no other cacao is known than this; the arillus around the seed is much esteemed for its delicious flavour and sweetness; it bears abundantly, on one tree (cultivated) I saw several hundreds of fruits but in a green state. I believe it to be a hardier species than *T. cacao* as it is a native of the lower mountain, while *T. cacao* is a native of the hotter plains. This species is often of the same habit and size as *T. cacao*. Hab. in dense woods .... Of this I was able to obtain ripe fruit." December 1845, *William Purdie sine num.* (TOPOTYPE in Herb. Kew).

Herrania kanukuensis *R. E. Schultes* in Caldasia no. 6 (1943) 11.

A duplicate type of *Herrania kanukuensis* at Kew (*A. C. Smith 3541*) has several leaflets which tend to be slightly irregularly dissected, suggesting a condition which approaches that of some specimens of *H. lemniscata* in which the leaflets are abnormally developed. In the original description of *Herrania kanukuensis*, the leaflets are described as "margine subintegra, saepe prope apicem subundulato-sinuato." In their fruit, however, these two concepts are clearly distinct. It is obvious that *Herrania lemniscata* represents a link between *H. laciniifolia* of Colombia and *H. kanukuensis* of British Guiana which is, in turn, probably allied to the several Amazonian species.

Herrania laciniifolia *Goudot ex Triana & Plan-*

EXPLANATION OF THE ILLUSTRATION

PLATE XXX. Schomburgk's field painting of *Lightia lemniscata*, tab. XLI in the Schomburgk collection of water colors in the British Museum.

Plate XXX

chon apud García-Barriga in Caldasia no. 2 (1941) 55, t. 1, 4.

Collections of *Herrania laciniifolia* are not frequent. It is unfortunate that a precise locality for *Kalbreyer 2047* is not available.

COLOMBIA: "New Granada, 4000 ft. Shrub, stem simple 10–12 ft. lf., yellowish, woody, rough, 3½ ft. l. 4 br., fl. on the stem below, red brown with bunch of greenish white petals, 7–8 in., threadlike, brownish white, pendulous." May 18, 1881, *Kalbreyer 2047* (Herb. Kew, 2 spec.).

Herrania lemniscata (*Schomb.*) *R. E. Schultes* in Caldasia no. 6 (1943) 13.

In 1943, when I validated the Schomburgk concept and made the new combination *Herrania lemniscata*, European collections were unavailable for study. Recently, additional and extensive material which I have seen in England indicates that *Herrania lemniscata* is a very distinct species. Schomburgk's original water colors, made in the field, are preserved at the British Museum of Natural History. Included in the collection is an excellent painting (tab. XLI) of this concept (as *Lightia lemniscata*) which is herein reproduced because it depicts with unusual accuracy the habit of the small tree. (Plate XXX)

Furthermore, the material at Kew has excellent fruiting specimens, so that it is now possible to describe the capsule:

Fructus longe pedunculatus (pedunculus robustus, glaber vel glabrescens, usque ad 4.5 cm. longus, 3 mm. in diametro), perfecte ovoideus, 7 cm. longus, 4 cm. in diametro, apice brevissime et abrupte cuspidatus, basi subrotundatus, omnino dense et minute stellato-pilosiusculus, sine pilis urticantibus ut videtur, decem-costatus quinque cum costis primariis, angustis subhumilibusque, 2 vel 4 (siccitate) mm. altis, 1–2 mm. crassis, subcultri-

formibus, atque quinque cum costis secundariis similibus, minoribus, pericarpio inter costas longitudinales valde reticulato-costato tenuissimo, maturitate probabiliter luteo. Semina plura quam sexaginta ut videtur, in circuitu triangularia vel angulato-ovata, complanata, 12×11×11 mm., plusminusve 4 mm. crassa, in pulpa alba inclusa.

Of the specimens cited below, fruits in mature condition are preserved in *im Thurn sine num.* (which I have chosen as the type of the fruit), *Rusby & Squires 252* and *Forest Department Brit. Guiana Record No. 4500.* The last of these three collections has a 6-costate fruit, an unusual and probably abnormal departure from the 5-parted condition of the genus.

British Guiana: "Banks of Barima River" *Schomburgk* (Herb. Kew, 3 spec.)—[Everard] *im Thurn sine num.* (Herb. Kew, fructus typus, 4 spec.).—"Upper Arawau River, Aruka River, N.W.D. Mixed forest in swamp and on rather swampy soil. Small tree, 20–30 ft., but told by Indians it grows larger. Trunk 4 in. diam. at 6 ft. from ground. Leaves alternate, large, compound, palmate, 6-lobed in specimens taken. Slender paired stipules at base. Flowers cauliferous at base of trunk. Arawak dialect: *bur-oo-ma.*" May 1929, *Martyn 61.* (Herb. Kew, 2 spec.).—"Essequibo River, White Creek, Groete Ck. 15 ft. high, soft-wooded tree from clearing with terminal, peltate, long-stalked lvs., pubescent below, br. velvety on petiole and midrib beneath; fr. cauliflorus, fascicled, 1–4 together, drooping, long-stalked ovoid-globose, acuminate with 6 major and 6 minor ribs and numerous lesser oblique ridges between ribs, greenish, the ribs darker, thinly bony with an inner pithy layer, seeds forming a soft, white oblong-globose mass divided into 6 segments shaped like orange flakes, each flake consisting of 3 seeds embedded in thin, sugary pulp with a very sticky coating to testa—testa pale brown finely pitted, wrinkled and veined—seed trigonous." *Forest Dept. British Guiana Field No. F1764, Record No. 4500* (Herb. Kew).

Venezuela: "Catalina, Lower Orinoco" 1896, *H. H. Rusby & Roy W. Squires 252* (Herb. Kew, 2 spec.).

Herrania purpurea (*Pittier*) *R. E. Schultes* in Caldasia no. 9 (1944) 333.

The following collections of *Herrania purpurea* em-

phasize the common occurrence of this representative of a South American genus in adjacent areas of Central America, as far north as the Republic of Nicaragua. The species appears to be concentrated especially in Panama.

The Colombian collection cited below is the second collection from Colombia and the South American continent. The first, *Schultes 5754*, (reported in Caldasia no. 11 (1944) 23, t. 1, 2), was from the region near Turbo. *Schultes & López 10464*, while from the same general area (the Golfo de Urabá), places *Herrania purpurea* much farther to the south.

COLOMBIA: Departamento de Antioquia, Golfo de Urabá, Villa Arteaga, Municipio de Pavorandocito. "Small tree 8 ft. tall." December 1948, *Richard Evans Schultes & Francisco López 10464.*

NICARAGUA: 1867, *Seemann sine num.* (Herb. Mus. Brit.).

PANAMA: "Chiriquí" [Rec'd.] June 1886, *J. H. Hart sine num.* (Herb. Kew). *Sutton Hayes sine num.* (Herb. Kew; Herb. Mus. Brit.) Canal Zone, near Madden Dam, "near sea level. Forest. Shrub, simple stem 10 ft.; fruits yellow." June 9, 1939, *A. G. H. Alston 8861* (Herb. Mus. Brit.; Herb. Gray).

DILLENIACEAE

Saurauia rigidissima *R. E. Schultes sp. nov.*

Arbor parva et pulcherrima ut videtur. Rami lignosi strigillosique cum pilis subhamulatis, fusco-ferrugineis, 4 mm. longis dense obtecti. Folia rigide coriacea, obovata, apice rotundata, basi cuneata, margine remotissime subdenticulata, 29–41 cm. longa, 12.5–16 cm. lata: infra (siccitate) aureo-brunnea, dense et minutissime granulosa, maximopere minutissime et subremote stellato-pilosa; supra (siccitate) brunneo-viridia, subnitida; venis crassis, hamulato, strigosis, supra planis, infra prominenter elevatis; petioli robustissimi, hamulato-strigosi, 4.5 cm. longi, 5 mm. crassi. Inflorescentiae erectae, foliis aequales vel longiores, multiflorae, dense paniculatae; bracteae pedicellos subtendentes minutissimae, triangu-

lares, 0.7 mm. longae, hispidulae. Alabastra globosa. Flores parvi, aperti 8–10 mm. in diametro. Sepala quinque, inaequalia; exteriora tria membranacea, ovata, apice rotundata, 5–6 mm. longa, 3 mm. lata, glaberrima, alba, inflexis cum marginibus; interiora duo membranacea, suborbicularia, 5.5 mm. longa, 4.5 mm. lata, alba. Petala quinque, membranacea, alba, rotundato-ovata, 6 mm. longa, 4.5 mm. lata. Stamina circiter 28, basi albo-barbata; filamenta 2 mm. longa. Antherae plusminusve 1.8 mm. longae. Ovarium globosum, stylis quinque filiformibus, 3 mm. longis, apice in stigmata leviter dilatatis. Fructus maturus adhuc ignotus.

The peculiar fragile texture of the highly coriaceous and rigid leaf of this new species distinguishes *Saurauia rigidissima* from the other known Colombian members of the genus. According to the field notes, the leaves are fragile even in life. There are also minor distinguishing characters in the hairs of the petiole and branch.

Colombia: Departamento del Valle, "Cordillera Occidental, Los Farallones, vertiente oriental: abajo de Almorzadero, bosque 2850–2880 m. alt. Arbolito. Hoja grande, coriacea, rígida, frágil, verde grisácea haz, verde claro envés. Cáliz verde pálido. Corola blanca," July 25, 1946, *J. Cuatrecasas 21716* (Type in Herb. Gray).

Flacourtiaceae

Mayna amazonica (*Martius ex Eichler*) *J. F. Macbride* in Field Mus. Publ. Bot. 13, pt. 4 (1941) 16.

Rather widespread in the Amazon drainage-area, *Mayna amazonica* extends up to the very slopes of the Andes in eastern Colombia. This is the second collection from the Comisaría del Putumayo (Schultes in Caldasia 3 (1945) 439). Among the Kofán Indians, the bark of the trunk of this small tree is used as an ingredient of curare.

Colombia: Comisaría del Putumayo, Río San Miguel ó Sucumbíos,

Conejo y alrededores frente a la Quebrada Conejo, alt. 300 m. "Nombre kofán: *tzá-he-vee-ko.* Tree." 2–5 abril, 1942, *Richard Evans Schultes 3515.*

Mayna pacifica (*Cuatrecasas* var. **pusilla** *R. E. Schultes var. nov.*

Frutex parvus, usque ad tres pedes altus, ab *Mayna pacifica* specialiter foliis minoribus (usque ad 35 cm. longis et 11 cm. latis), infra glabris atque fructu minore (solum 4 cm. longo et 2.5–3 cm. in diametro) cum alis membranaceis profunde fimbriato-dentatis differt. In provincia Chocó nomen vulgaris: "clavo."

This newly described variety differs from *Mayna pacifica* Cuartr. in being much smaller in all its parts and, most conspicuously, in having elaborate and deeply fimbriate wings on the fruit. In *Mayna pacifica*, the fruit is two and one half times as long as in var. *pusilla* and the wings are strongly and irregularly dentate, not approaching the echino-fimbriate condition found in var. *pusilla.*

Mayna pacifica var. *brachycarpa* Cuatr. is also larger than var. *pusilla*, and the wings of its fruit are barely conspicuous.

Mayna pacifica and the var. *brachycarpa* are native to the Pacific slopes of the cordillera in the Departamentos del Cauca and Valle, respectively, slightly south of the general region of Quibdó, where the type of var. *pusilla* was collected.

Colombia: Intendencia del Chocó, Headwaters of Río Tutunendó, east of Quibdó. "*Clavo.* Slender shrub 2–3 ft. Flw. and fruit white. Flw. faintly scented." May 20–21, 1931, *W. A. Archer 2195.* (Type in U. S. Nat. Herb. No. 1518794).

Thymeleaceae

Schoenobiblus peruvianus *Standley* in Field Mus. Publ. Bot. 11 (1936) 169.

EXPLANATION OF THE ILLUSTRATION

PLATE XXXI. SCHOENOBIBLUS PERUVIANUS *Standley*. 1, fruiting branch, approximately one half natural size. 2, fruit, approximately natural size.

Plate XXXI

SCHOENOBIBLUS

peruvianus

Standl.

Schoenobiblus peruvianus has hitherto not been recorded from Colombia. The only other representative of this genus in Colombia is *Schoenobiblus coriaceus* Domke, which has been found on Sierra Santa Marta at an altitude of 4,500 feet.

Schoenobiblus peruvianus is a very important ingredient in the arrow-poisons of the Kofán Indians of the Putumayo. Both the fruits and the root are employed. This is apparently the first report of a member of the *Thymeleaceae* as an ingredient of curare.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Conejo y alrededores, frente a la Quebrada Conejo, alt. 300 m. "Large shrub. Root furnishes one of the poisons for curare." 2–5 abril, 1942, *Richard Evans Schultes 3486*.—Same locality. "Small shrub. Poison: crushed fruits an ingredient of curare." 2–5 abril, 1942, *Richard Evans Schultes 3521*.—Same locality. "Poison. Fruits used in making curare. Shrub." 2–5 abril, 1942, *Richard Evans Schultes 3655*.—Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Santa Rosa y los alrededores, alt. 380 m. (?). "Roots and fruits used in Kofán curare preparation." 7–8 abril, 1942, *Richard Evans Schultes 3613*

SAPOTACEAE

Lucuma dolichophylla *Standley ex Llewelyn Williams* (sine diagn. lat.) in Field Mus. Publ. Bot. 15 (1936) 411.

Arbor 45–70 pedes alta, recto cum trunco plusminusve cylindrico, 8–20 poll. in diametro, ramo inferiore 12–35 pedes ab humo. Cortex extus atropurpureo-fuscus, dulce cum latice, intus grosse fibrosus. Flores parvi albique. Fructus rotundatus, indumento brunneo velutinoque maturitate lutescenti obtectus, esculentus.

This concept was described in English without a Latin diagnosis in Williams' "Woods of northeastern Peru." The name is here validated by rendering the English description into Latin.

Strychnos brachiata *Ruiz & Pavon* Fl. Peru. et Chil. 2 (1799) 30.

This species, known apparently only from subandean Peru and Bolivia (Krukoff and Monachino in Brittonia 4 (1942) 269), is now registered from Colombia (Krukoff and Monachino in Bol. Téen. Inst. Agron. Norte 12 (1947) 10) on the basis of the following collection.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Santa Rosa y los alrededores. Nombre kofán: *se-hé-pa*. "Vine. Root used in preparation of arrow poison." 7–8 abril, 1942, *Richard Evans Schultes 3602*.

Strychnos Erichsonii *Richard Schomburgk* Faun. Fl. Br. Guiana (1848) 1082, nomen; ex Progel in Martius Fl. Bras., 6, pt. 1 (1868) 274.

An Amazonian species, *Strychnos Erichsonii* was collected in Brazil (Ducke in Bol. Téen. Inst. Agron. Norte 3 (1945) 14) near the Colombian frontier, and was reported by Krukoff and Monachino (in Caldasia 4 (1946) 46) as one of the species to be expected in the Amazonian regions of Colombia. The collection cited below establishes the occurrence of the species in the southwesternmost sector of the Colombian Amazon area. It is known also from British and Dutch Guiana and Venezuela.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Conejo y los alrededores, en frente de la Quebrada Conejo. Nombre kofán: *ir-rro-chee*, 2–5 abril, 1942, *Richard Evans Schultes 3524*.

Strychnos Jobertiana *Baillon* in Adansonia 12 (1879) 367.

This species of *Strychnos* has apparently not been collected hitherto from Colombia. Known from Amazonian Peru, Ecuador and Brazil, it was first indicated as prob-

ably occurring also in Colombia by Krukoff and Monachino in Caldasia 4 (1946) 45. The Canelos Indians of Ecuador use the bark of the stem and roots in preparing curare (Krukoff and Monachino in Brittonia 4 (1942) 282).

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Conejo y los alrededores, frente a la Quebrada Conejo. Nombre kofán: *ir-rro-chee.* "Bark of root used in curare formula." 2–5 abril, 1942, *Richard Evans Schultes 3523.*—Intendencia del Amazonas, Río Loretoyacu, November 1946, *George A. Black & Richard Evans Schultes 46–262.*

Strychnos Peckii *B. L. Robinson* in Proc. Am. Acad. 49 (1913) 504.

This collection establishes the occurrence of *Strychnos Peckii* in the Colombian Amazonas (Krukoff and Monachino in Bol. Téen. Inst. Agron. Norte 12 (1947) 13). Hitherto known only from Colombia through one collection from the Valle del Cauca (Krukoff and Monachino in Lloydia 9 (1946) 65), it was to be expected as an element of the Amazonian flora. It ranges very widely, from Guatemala to Brazil and Bolivia (Ducke loc. cit. 14).

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Santa Rosa y los alrededores. Nombre kofán: *se-hé-pa.* "Root used in curare preparation. Small tree." 7–8 abril, 1942, *Richard Evans Schultes 3601.*

Strychnos rondeletioides *Spruce ex Bentham* Journ. Linn. Soc. 1 (1856) 104.

Strychnos rondeletioides has been known from Colombia hitherto through material collected along the Río Vaupés (Krukoff and Monachino in Caldasia 4 (1946) 43). *Schultes 3829* was collected in the southernmost sector of the Colombian Amazon drainage area. The species also occurs in Amazonian Bolivia, Brazil and Peru, as well as in Venezuela (Ducke loc. cit. 11).

COLOMBIA: Intendencia del Amazonas, Río Karaparaná, entre las bocas y El Encanto, alt. ca. 150 m. "Bush. Fruit blue-black or orange-red." 22–28 mayo, 1942, *Richard Evans Schultes 3829*.

SOLANACEAE

Solanum apaporanum *R. E. Schultes sp. nov.*

Since I have been unable to find any material of Solanum from the Amazon Valley to match this curious concept, I am describing it as new.

Fruticulus scandens. Rami teretes, glabri, spinosi, tenui cum cortice cinereo-fusco. Ramuli sordide fusco-pulverulenti. Folia mediocria, brevissime petiolata, subchartacea, elliptica, integra, apice longissime acuminata, basi cuneata, aequalia, 3.5–7.5 cm. longa, 1.5–2.3 cm. lata, supra sordide fusco-viridia, aspera, omnino dense et minute stellato-pilosa, subtus viridia pallida, densissime stellato-pilosa, nervo centrali retrorso-spinoso; petioli 2–4 mm. longi. Inflorescentia umbellata, pauciflora, pedicellis comparate robustis, rectis, 7–10 mm. longis, densissime fusco-pilosis. Alabastrum 4 mm. longum. Calyx omnino densissime stellato-pilosus, lobis breviter acutis, stellato-pilosis. Corolla profunde lobata extus stellato-pilosa, lobis anguste triangulari-acutis, 8 mm. longis, basi 2 mm. latis, membranaceis, albis, valde patentibus. Antherae conspicuae, flavae, 6–8 longae, apice poriferae. Bacca perfecte globosa (sine rostro), vivo 1–1.3 cm. in diametro, nitidissima, aureo-rubens.

COLOMBIA: Comisaría del Vaupés, Macaya-Ajaju River confluence. Mount Chiribiquete. Quartzite base. Summit 800–1200 ft. above forest floor, 1700–2100 ft. above sea level. "Spiny vine-shrub. Fruit orange. Flowers white, anthers yellow." May 15–16, 1943, *Richard Evans Schultes 5406*. (TYPE in Herb. Gray.)

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, JUNE 24, 1949 VOL. 13, NO. 10

PLANTAE COLOMBIANAE XI

DE PLANTIS PRINCIPALITER COLOMBIAE VALLIS AMAZONICAE OBSERVATIONES

BY

RICHARD EVANS SCHULTES[1]

STUDY of recently made collections of plants, chiefly from the Amazon watershed of Colombia, has brought to light a number of data which contribute to our knowledge of the flora of the northwesternmost reaches of the Amazon system. A few of the collections represent concepts which apparently have not hitherto been described. Others are noteworthy, since they alter or increase our understanding of plant distribution.

I have to thank Dr. Lyman B. Smith for determining the Cyperaceae and Bromeliaceae; Mr. Charles Schweinfurth, who identified the orchids; and Dr. Robert C. Foster for his attention to tiliaceous and lythraceous species.

CYPERACEAE

Cephalocarpus Dracaenula *Nees* in Martius Fl. Bras. 2, pt. 1 (1842) t. 18.

Cephalocarpus Dracaenula, a sedge which superficially resembles a Navia, was collected in La Pedrera (Cupatí) by Martius in 1820. It was collected the second time

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nearly a century later at the same locality by Ducke who reported (in La Géogr. 30 (1914–15) 365-372) that among the strange plants on the rocks at the summit of the Cerro de La Pedrera "on remarque. . . . une très curieuse Cypéracée inconnue ailleurs, le *Cephalocarpus Dracaenula* Nees."

COLOMBIA: Intendencia del Amazonas, Río Caquetá, La Pedrera. April 1944, *Richard Evans Schultes 5858*.

BROMELIACEAE

Aechmea corymbosa (*Mart.*) *Mez* in Martius Fl. Bras. 3, pt. 3 (1892) 316.

The type of this species was collected by Martius on the Río Caquetá of Colombia near the Brazilian boundary. *Schultes 5377* greatly extends to the northwest the known range of this species.

COLOMBIA: Comisaría del Vaupés, forest between Apaporis and Vaupés Rivers, path from Puerto Naré to Victoria. Alt. about 300 m. "Epiphyte. Flowers white. Bracts scarlet. Very fragrant." April 10–17, 1943, *Richard Evans Schultes 5377*.

Aechmea Schultesiana (*Mart.*) *Mez* in Martius Fl. Bras. 3, pt. 3 (1892) 334.

In 1942, Smith indicated (in Caldasia no. 1 (1942) 13) that *Cuatrecasas 7250* from Mitú in the Comisaría del Vaupés was the first collection of *Aechmea Schultesiana* from Colombia.

Since that date, three additional collections from very far distant points in Colombia have been made, indicating that the species is to be found in nearly all sectors of the Republic.

Aechmea Schultesiana is known from Colombia, Peru, Venezuela and Costa Rica. *Schultes 3610* was collected on the Colombian-Ecuadorean border, so the species must be also assigned to Ecuador.

COLOMBIA: Comisaría del Putumayo, Río Sucumbíos, Santa Rosa y alrededores. Alt. 380 m.? "Bracts red. Epiphyte." April 7–8, 1942,

Richard Evans Schultes 3610.—Departamento de Antioquia, selva veranera siempreverde cerca de Porcesito en el valle del río Medellín, alt. aprox. 1100 m., April 16, 1946, *W. H. Hodge 6793.*—Departamento del Norte de Santander, Bellavista on Pipeline. September 15, 1946, *M. B. & R. Foster 1696.*

Aechmea tillandsioides (*Mart.*) *Baker* var. **Kienastii** (*E. Morr ex Mez*) *L. B. Smith* in Caldasia no. 5 (1942) 5.

This variety is known from many parts of Colombia and from Venezuela. Two collections from the Amazon watershed have been cited by Smith (loc. cit.): *Pérez-Arbeláez & Cuatrecasas 6758* from Mitú, and *Cuatrecasas 8832* from Florencia. *Schultes 5413* extends the species to the vast drainage-area of the Apaporis River.

COLOMBIA: Comisaría del Vaupés, Macaya-Ajaju River confluence. Mount Chiribiquete. May 15–16, 1943. *Richard Evans Schultes 5413.* —Comisaría del Vaupés, Río Macaya, vicinity of Cachivera del Diablo. "Bracts red, fruits white." May 14, 1943, *Richard Evans Schultes 5440.*

Navia caulescens *Martius ex Schultes fil.* Syst. 7 (1830) 1195.

The type of this very restricted endemic was collected by Martius at Araracuara and on the mountain at Cupatí (La Pedrera) on the Río Caquetá. It was collected again near the top of the Cerro de La Pedrera by Ducke in 1912.

In a summary of plants collected on this trip at La Pedrera, Ducke (loc. cit. 365–372) stated of this bromeliad: "Sur les grands blocs de pièrre abonde une Broméliacée très curieuse, la *Navia caulescens* Mart., découverte ici en 1820 et qui n'avait jamais été ensuite retrouvée." *Schultes 5859*, also from the top of the mountain at La Pedrera, represents the fourth collection of this strikingly distinct endemic.

COLOMBIA: Intendencia del Amazonas, Río Caquetá, La Pedrera. April 1944, *Richard Evans Schultes 5899.*

Dictyostega orobanchioides (*Hook.*) *Miers* var. **parviflora** (*Benth.*) *Jonker ex Pulle* in Kon. Ver. Kolon. Inst. Amsterdam Med. 30 (1938) 185.

This interesting saprophytic plant is widespread, and is known from Trinidad, Amazonian Brazil, Venezuela, British Guiana, Surinam and Colombia. *Schultes 5672* is the third collection from Colombia and the second from Colombia's Amazon drainage-area. Jonker cites a collection from Sur de Santander; *Cuatrecasas 7177* from Cerro de Circasia on the Río Vaupés above Mitú is also referable to this variety.

COLOMBIA: Comisaría del Caquetá, Cerro del Castillo, Río Apaporis, alt. 350–1000 ft. July 27, 1943, *Richard Evans Schultes 5672*.

ORCHIDACEAE

Epidendrum imatophyllum *Lindley* Gen. et Sp. Orch. Pl. (1831) 106.

Epidendrum imatophyllum is a very common tropical American orchid. It has apparently been collected twice in Colombia: *Haught 1419* from Santander and *Schultes 6729*, the first from the Colombian Amazonia.

COLOMBIA: Intendencia del Amazonas, Río Loretoyacu. "Flowers purple." October 20–30, 1945, *Richard Evans Schultes 6729*.

Epidendrum nocturnum *Jacquin* var. **minus** *Cogniaux* in Bull. Soc. Roy. Bot. Belg. 43 (1907) 323.

Epidendrum nocturnum var. *minus* was described from material collected by Ule in Loreto, Peru. It is exceedingly common in the adjacent Amazonian areas of Colombia.

COLOMBIA: Intendencia del Amazonas, Río Karaparaná, entre las bocas y El Encanto. "Epiphyte. Flowers cream-yellow. Lip white. Fragrant." May 22–28, 1942, *Richard Evans Schultes 3845*.

Habenaria monorrhiza (*Sw.*) *Reichenbach fil.* in Ber. Deutsch. Bot. Gesell. 3 (1885) 274.

Known from Peru (where it is very common), Ecuador, Venezuela and Puerto Rico, this beautiful Habenaria has apparently hitherto been collected but twice in Colombia: *Klug 1662* from Umbría in the Putumayo (only a few miles from the locality of *Schultes & Smith 3005*) and *Lawrance 206* from Mt. Chapón in Boyacá, the former from an altitude of 325 meters, the latter from 1036 meters.

COLOMBIA: Comisaría del Putumayo, Mocoa y alrededores al norte, alt. 750–850 m. "Flowers white. Growing in sand on bank." December 3–7, 1942, *Richard Evans Schultes & C. Earle Smith 3005*.

Maxillaria rufescens *Lindley* in Bot. Reg. (1836) t. 1848.

A widespread species, *Maxillaria rufescens* has apparently not been collected previously from Colombia. Known from Trinidad, Honduras, Guatemala, British Honduras, Nicaragua, Costa Rica and Cuba, it is apparently very common in Central America and the Antilles. It is known also from Brazil, but collections are rare.

COLOMBIA: Intendencia del Amazonas, Río Putumayo, carretera entre Caucaya y La Tagua. "Epiphyte." May 17, 1942, *Richard Evans Schultes 3791*.

Odontoglossum coronarium *Lindley* Fol. Orch. Odontog. (1852–59) 21.

Odontoglossum coronarium has hitherto been known from Panama, Colombia, Peru, and, probably, Ecuador.

COLOMBIA: Comisaría del Putumayo, Valle de Sibundoy, Porotoyaco, alt. about 2250 m. "Sepals and petals red-brown, yellow in spots. Lip yellow; lower half of lip red-brown. Column red-brown and yellow." December 16, 1942, *Richard Evans Schultes & C. Earle Smith 3150*.

Sobralia rosea *Poeppig & Endlicher* Nov. Gen. ac Sp. 1 (1836) 54, t. 93.

Schultes 3559 is the second collection from southern Colombia of this orchid which is widespread on the eastern slopes of the Andes.

COLOMBIA: Comisaría del Putumayo, Río San Miguel ó Sucumbíos, Santa Rosa y alrededores. "Flowers white, tip of column purple. Kofán Indian name: *ku-pu-ñú-mem-ba*. April 7–8, 1942, *Richard Evans Schultes 3559*.

Xylobium squalens (*Lindl.*) *Lindley* var. **gracile** (*Schltr.*) *C. Schweinfurth* in Bot. Mus. Leafl. Harvard Univ. 11 (1944) 198.

This is apparently the first collection from Colombia of *Xylobium squalens* var. *gracile*, hitherto known only from Ecuador.

COLOMBIA: Comisaría del Putumayo, Páramo de Tambillo, nordeste del Valle de Sibundoy. "Flowers cream with red specks." December 13–14, 1942, *Richard Evans Schultes & C. Earle Smith 3094*.

MORACEAE

Perebea lecithogalacta (*R. E. Schultes*) *R. E. Schultes comb. nov.*

Castilla Ulei Warb. forma *lecithogalacta* R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1946) 128.

Further investigation has indicated that this concept, which was referred to *Castilla Ulei* as a form, represents a new species of the related genus *Perebea*.

The genus *Perebea* has hitherto not been considered as a commercial source of rubber, but *P. lecithogalacta* is felled indiscriminately with *Castilla Ulei* in the upper reaches of the Vaupés River in Colombia for the production of "caucho negro." The latex, when it flows from the wound, is first a deep cream color but rapidly becomes a bright canary yellow.

It is evident that the "caucho negro" of this area of

Colombia is a mixture of *Castilla* and *Perebea* latex, and it may well be that other genera furnish a part of this rubber so eagerly sought for during the recent war.

Proteaceae

Roupala colombiana *R. E. Schultes sp. nov.*

Arbor quindecim ad viginti quinque pedes alta, apparenter ramosa. Ramuli teretes, densissime et molliter rufo- vel cinereo-tomentosi. Folia alterna, elliptico-ovata, apice rotundato-subacuta (sed nunc subrotundata vel obscure acuta), basi late cuneata vel rotundata (*Killip & Smith 19737*), valde marginata, integra, vel saepe obscure sinuata (*K. & S. 19737*), valde coriacea, maturitate 7–10 cm. longa, 4.5–6.5 cm. lata (13 cm. longa, 10 cm. lata in *K. & S. 19737*), supra minute fusco-tomentella, nervorum centralium nervos secundarios versus dense sordide cinereo-tomentosa, venis plerumque elevatis et bene conspicuis, infra omnino densissime et molliter rufo-tomentosa (folia juniora multo rufiora), venis non valde elevatis; petioli dense tomentosi, 1–2.5 cm. longi. Racemi multiflori, axillares, quam folia multo longiores, aliquid rigidi, usque ad 15 cm. longi vel longiores, rhachide floribusque dense rufo-tomentosis. Bracteae minutissimae, caducae. Alabastri densissime rufo-tomentelli. Calycis lobi valde clavati, usque ad 11–12 mm. longi, contorti. Stylus longior, usque ad 12 mm. longus. Ovarium subcompresso-ovoideum, densissime et grossiuscule tomentosum, 2× 1.7×1.5 mm. Folliculus obliquus, elliptico-oblongus, valde compressus, apice attenuato-acutus, cinereo- vel fusco-tomentellus.

Vegetatively, *Roupala colombiana* resembles *R. saxicola*, but the reddish or rusty indumentum of the former is very much denser and softer than that of the latter. There is likewise a difference in the shape of the leaves. The flowers and the peculiarly strict, very long and

rather remotely flowered inflorescence exhibit further differences, and the fruits of the two species are entirely distinct, those of *Roupala saxicola* being fully rounded, apically obtuse, and glabrous, while those of *R. colombiana* are complanate, apically acute, and tomentulose.

COLOMBIA: Departamento Norte de Santander (Eastern Cordillera) between Mutiscua and Pamplona; alt. 2700 m. "Tree 15–25 ft., sepals cream white. Edge of woods." February 23, 1927, *E. P. Killip & Albert C. Smith 19762* (TYPE in Herb. Gray).—Same locality and date. *E. P. Killip & Albert C. Smith 19737.*—Departamento Norte de Santander, Cordillera oriental, vertiente oriental, Pamplona, Quebrada de Cariongo, matorrales, 2500 m. alt., 26 julio 1940, *J. Cuatrecasas & H. García-Barriga 10242.*

Roupala saxicola *R. E. Schultes sp. nov.*

Frutex usque ad duodecim vel quindecim pedes altus, ramosus. Rami teretes, nigro-cinereo cum cortice; ramuli densissime et molliter rufo-tomentosi. Folia pinnatipartita, 25–28 cm. longa, oppositi- vel subopposita-foliola, cum 6–10 foliolis, petiolulata (petioli usque ad 5 mm. longi); foliola elliptico-oblonga, apice rotundata, basi cuneata, marginata, integerrima, coriacea, maturitate 7.5–11 cm. longa, 4.5–5.5 cm. lata, supra viridia, minute reticulata, minute tomentella nervorum centralium nervos secundarios versus dense rufo-tomentosa, venis vix elevatis, infra omnino densissime et molliter rufo-tomentosa, venis valde elevatis. Racemi densiflori, axillares, quam folia breviores, rigidissimi, usque ad 14 cm. longi, cum rhachide floribusque dense rufo-tomentosis. Bracteae minutissimae, caducae. Calycis lobi valde clavati, cucullati, 8–8.5 mm. longi, valde contorti et patentes. Stylus robustus, 9–10 mm. longus, paulo arcuatus; stigma capitato-clavatum. Ovarium sessile, grosse rufo-villosum, elongato-ovoideum. Folliculus (*Schultes 5457*) ovali-oblongus (noncompressus), glaber, rufo-aureus vel aureus, apice rotundatus, pedicello brevissimo, 3.2–3.5×2.2×2 cm.

Roupala saxicola differs from other species which have

a soft, dense, red indumentum by having perfectly entire, slightly marginate leaves. It is also striking in having a short and very dense inflorescence. The unusually broad and rounded leaflets of this species and also the fully rounded (not flattened) fruits are distinct in the genus.

COLOMBIA: Comisaría del Vaupés, Upper Apaporis Basin, Macaya River, Mount Chiribiquete. Sandstone. Xerophytic conditions. Savannah. Alt. 400–1200 ft. above forest floor or 1300–2100 ft. above sea-level. "Shrub up to 12 ft. Flowers greenish yellow. Growing on summit." January 18, 1944, *Richard Evans Schultes 5744*. (TYPE in Herb. Gray).—Same locality. "Small tree. Fruit yellow." May 15–16, 1943, *Richard Evans Schultes 5457*.

POLYGONACEAE

Triplaris Pavonii *Miessner* in DC. Prodr. 14 (1856) 172.

This widely distributed tree is one of the commonest species on floodable river-banks in the upper Apaporis River drainage-area.

COLOMBIA: Comisaría del Vaupés, confluence of Macaya and Ajaju Rivers, Puerto Hevea. Alt. about 300 m. "Bracts of calyx red. Tree." July 1943. *Richard Evans Schultes 5576*.

LEGUMINOSAE

Cynometra Zamorana *R. E. Schultes sp. nov.*

Arbor magna et robustissima, usque ad centum pedes alta. Truncus columnaris, duo pedes in diametro, brunneo cum cortice crasso. Foliola unijuga, obliqua, elliptica, apice breviter cuspidato-acuta, basi cuneata, saepe obscure marginata, coriacea, supra nitidissima, infra nitida, viridia, utrinque glabra maxima pro parte 13.5 cm. longa, 5–5.5 cm. lata; venae secundariae saepissime quindecim vel sedecim, supra non conspicuae sed infra valde elevatae, nervo centrali rufo; petioli crassiores. Racemi axillares, foliis saepius aequales, minutissime villosi pubi molli patenti, rhachide robusta, 6–7 cm. longa, pedi-

cellis crassis 8–10 mm. longis. Bracteae subtendentes caducissimae. Flores ignoti. Legumen subsessile, compressum, oblique ovoideum, minutissime cuspidatum, basi valde fusco-tomentosum, rufo-brunneum, conspicue rugosum, sublignosum vel lignoso-coriaceum, plerumque 3.7–4.3 cm. longum, 2.2–3 cm. latum, 1.8 cm. crassum. Semen transverse oblongum, arillatum, 2.5 cm. longum, 1.8 cm. latum, 1.2 cm. crassum, nigrum, nitidum. Arillus crassus, vivo siccus, pulverulentus, subluteus, gustatu dulcis.

Cynometra Zamorana is apparently not closely allied to any known species of this interesting genus. It is distinctive at once because of the large size of its leaves and its legumes. The Indians of the upper Vaupés River eat the dry, powdery, sweet, pulpy aril of the seed and use the trunks of the large tree in the construction of rafts. Among the Spanish-speaking inhabitants of the same region, *Cynometra Zamorana* is called *coca*, the same term which is widely used to refer to the completely unrelated narcotic plant *Erythroxylon Coca* Lam.

I have named this beautiful, majestic tree in memory of one of the boys who penetrated the upper Apaporis River with me on my first expedition to that uninhabited area. Armando Zamora, 19, a native of the town of San Martín, Intendencia del Meta, lost his life by drowning when he was swept through the lowermost rapids in the Macaya River on April 7, 1943, while performing his duties on that expedition.

Colombia: Comisaría del Vaupés, Río Macaya, vicinity of Cachivera del Diablo. "*Coca*. Very tall tree (90 ft.) in swampland. Fruits reddish brown. Basal diameter 1½–2 ft. Bark reddish brown, rough. Fruit edible, sweet, reddish." May 14, 1943, *Richard Evans Schultes 5429* (Type in Herb. Gray).—Comisaría del Vaupés, Upper Apaporis Basin, region of confluence of ríos Macaya and Ajaju (Puerto Hevea). Forest. Alt. ca. 900 ft. "Tree 100 ft. tall. Bark brown, rough. Seed-pulp brown, edible, sweet. Fruit red-brown." May 1943, *Richard Evans Schultes 5424*.

Tiliaceae

Heliocarpus popayanensis *HBK.* Nov. Gen. et Sp. 5 (1821) 341.

A very common and rather widespread tree, *Heliocarpus popayanensis* has apparently not previously been reported from Amazonian Colombia.

Colombia: Comisaría del Putumayo, Mocoa y los alrededores al norte. Alt. 750–850 m. "Small tree. *Balso blanco. Urtequillo blanco.*" Dec. 3–7, 1942, *Richard Evans Schultes 2077.*

Bombaceae

Bombax coriaceum *Martius & Zuccarini* Nov. Gen. et Sp. 1, 93 in obs.; K. Schumann in Martius Fl. Bras. 12, pt. 3 (1886) 219; emend. Dugand in Caldasia no. 10 (1944) 435.

This collection extends the known range of the diminutive *Bombax coriaceum* far to the east and indicates that probably the species will be collected in Venezuela. The type came from Araracuara on the Río Caquetá, where Martius found it in 1820 on the sandstone savannas which are so extensive there. More than one hundred and twenty years elapsed before it was rediscovered (*Schultes 5461* and *5616*) on the sandstone hills in the upper Apaporis basin—hills geologically and geographically the same as those at Araracuara two hundred kilometers distant—and on sandstone savannas at the headwaters of the Cuduyarí and Cubiyú (*Allen 3090*) about two hundred kilometers to the east of the Apaporis locality (Dugand in Caldasia no. 8 (1943) 298; no. 10 (1944) 435). The present collection (*Schultes & López 9342*) extends the known range another two hundred and fifty kilometers eastwards, and places *Bombax coriaceum* in the great Río Negro basin. This still further strengthens our belief (based upon the study of the distribution of a number of plants of eastern Colombia and southern

Venezuela) in the close geological and floristic relationship or even the identity of the now discontinuous sandstone remnant hills and savannas which, crossing the Colombian Amazon drainage-area in an arc from southern Venezuela westward and southwestward, appear to be an ancient outlier of the formidable Venezuelan-Guianan land-mass.

COLOMBIA: Comisaría del Vaupés, Río Negro, San Felipe (opposite San Carlos, Venezuela). Caatinga. "Low shrub 3 ft. tall. Leaves very coriaceous." December 12, 1947, *Richard Evans Schultes & Francisco López 9342*.

FLACOURTIACEAE

Mayna longifolia *Poeppig & Endlicher* Nov. Gen. ac Sp. 3 (1845) 64, t. 271.

Although *Mayna longifolia* is not uncommon in Amazonian Peru and Brazil, it does not seem to have been reported from eastern Colombia. A variety (var. *phasmatocarpa*) has been described from the upper reaches of the Vaupés River (Schultes in Bot. Mus. Leafl. Harvard Univ. 12 (1946) 125).

COLOMBIA: Comisaría del Amazonas, Trapecio amazónico, Loretoyacu River, alt. about 100 m. "Small tree. Fruit white." September–November 1944, *Richard Evans Schultes 6381*.

BEGONIACEAE

Begonia lutea *Smith & Schubert* in Caldasia 4 (1946) 11.

Begonia lutea is a widespread, though rare, species in eastern Colombia, as indicated by the four collections which have been made of this species. *Schultes & López 10062* represents the easternmost limit of its known range. The type or westernmost collection (*Pennell 1537*) was made near Villavicencio in the foothills of the Andes. *Cuatrecasas 7547*, from the Río Guayabero in the Vaupés, and *Schultes 5658*, from the upper Apaporis

basin, are intermediate and show that this species is probably an ancient remnant now represented discontinuously in eastern Colombia.

COLOMBIA: Comisaría del Vaupés, Río Guainía, Río Naquiení, Cerro Monachí. "On shady, rocky cliff. Flowers yellow." June, 1948. *Richard Evans Schultes & Francisco López 10062.*

LYTHRACEAE

Cuphea cathargenensis (*Jacq.*) *Macbride* in Field Mus. Publ. Bot. 8 (1930) 124.

Cuphea cathargenensis has been collected in nearly all parts of Colombia but has hitherto apparently not been recorded from the Amazon watershed.

COLOMBIA: Comisaría del Putumayo, Valle de Sibundoy, alt. ca. 2250 m. "Flowers violet." Feb. 12, 1942, *Richard Evans Schultes 3201.*

Cuphea racemosa (*L.f.*) *Sprengel* Syst. 2 (1825) 455.

This species has been collected very frequently along the entire Andean cordillera of Colombia in Antioquia, Caldas, El Valle, Cauca, and possibly in Nariño. *Schultes & Smith 2097* seems to be the first collection from the Amazon watershed. The plant is used, in the form of a decoction, as a diuretic by the Inga Indians of Mocoa.

COLOMBIA: Comisaría del Putumayo, Mocoa. Alt. 750–850 m. "Diuretic. Flowers purple. Inga name: *i-spa-na-nai-ambe.* Dec. 3–7, 1942, *Richard Evans Schultes & C. Earle Smith 2097.*

Cuphea strigulosa *HBK.* Nov. Gen. et Sp. 6 (1823) 204.

Cuphea strigulosa is frequent in the Andes of Peru, Ecuador and Colombia. The collection cited below is the first from Huila and the southernmost from Colombia.

COLOMBIA: Departamento del Huila, Pitalito, Quinche, open fields. Alt. 1300 m. December 30, 1942, *Richard Evans Schultes & M. Villarreal 5119.*

Graffenrieda fantastica *R. E. Schultes & L. B. Smith sp. nov.*

Frutex usque ad duodecim pedes altus. Truncus valde contortus, nigro cum cortice 1–1.5 cm. crasso. Rami teretes, crassissimi et molles, vivo rufo-brunneo cum cortice chartaceo, nitidissimo, decorticanti, siccitate cinereo-nigro. Folia rotundato-ovata, basi subcordata, apice subrotundata vel obscure subacuta, marginata, quinquenervia, nervis transversalibus utrinque obscuris, siccitate atrofusca vel luteo-viridia, vivo atroviridia, omnino glabra et nitidissima, 8–10 cm. longa, 6–8 cm. lata, longe petiolata; petioli teretes, 3 cm. longi, dure et crasse coriacea. Paniculae terminales, multiflorae, quam folia multo longiores. Flores albi, usque ad 5 mm. lati. Calycis tubus suboblongus, 1–1.5 mm. altus, basi rotundatus, apice paulo dilatatus, omnino glaber, fusco-purpureus, profunde trilobatus, lobis triangularibus, apice rotundatis, Antherae flavae, subulatae, falcato-recurvatae, 2–3 mm. longae, 0.5 mm. crassae, loculis arcuato-crispatis apice longe attenuatis, connectivo in parte basali breviter calcarato. Petala ovata, margine paulo irregularia, erecto-patula, membranacea, alba, 3–4.5 mm. longa, 2–2.5 mm. lata. Ovarium conspicue quinquesulcatum, superne rotundatum, 1.5–2 mm. longum. Stylus luteus, gracilis, 6–7 mm. longus, stigmate capitellato. Capsula fuscentia, ovoidea, apice valde truncata, 3.5–4 mm. longa, 2.5–3 mm. in diametro.

This extraordinary bush, growing in the most exposed and inhospitable places on Mount Chiribiquete, is certainly one of the most outstandingly distinct species of the genus. It does not appear to be closely related to any known species, perhaps approaching most closely *Graffenrieda sessilifolia* Triana, which is found on Mount

Roraima in southern Venezuela. Both are highly adapted to xerophytic conditions, having thick, coriaceous leaves. *Graffenrieda fantastica* is further adapted to xerophytic conditions by having the young and crassulent branchlets tightly covered with a chartaceous and apparently impervious bark which, when broken, easily peels from the stem.

Graffenrieda fantastica is one of the dominant shrubs on the long, flat sterile sandstone summit of Mount Chiribiquete where it forms dense stands of at least one thousand per hektar, intermingled with *Hevea nitida* var. *toxicodendroides Ficus chiribiquetensis, Plumeria* sp., *Bombax coriaceum, Roupala saxicola, Gongylolepis maroana* and *Senefeldera chiribiquetensis.* The collection *Schultes 5620* was formerly identified and reported (in Caldasia 3 (1944) 121–130; in Chron. Bot. 9 (1945) 123–127), as representing *Miconia paradoxa* Triana, a vegetatively very similar xerophyte from the nearby sandstone hills of Araracuara.

COLOMBIA: Comisaría del Vaupés, Upper Apaporis Basin, Río Macaya, Cerro Chiribiquete, alt. about 1200 ft. above forest floor or 2100 ft. above sea-level. "On sterile sandstone top of mountain. Leaves fleshy. Flowers white, very fragrant. Bush up to 12 ft., very scraggly. Bark basally rugose, grey; terminally glossy, red-brown." July 24, 1943, *Richard Evans Schultes 5620* (TYPE in Herb. Gray; DUPLICATE TYPES in U.S. Nat. Herb., Herb. Nac. Colomb.).—Same locality. "Scraggly bush, 8–10 ft. tall." May 15–16, 1943, *Richard Evans Schultes 5467.*

GENTIANACEAE

Chelonanthus chelonoides (*L.f.*) *Gilg* in Engler et Prantl. Pflanzenfam. 4, Abt. 2 (1895) 98.

This heliophile is sometimes found in extraordinary abundance on the open savannas of the sandstone mountains of the upper Apaporis basin.

Colombia: Comisaría del Vaupés, Macaya-Ajaju River confluence, Mount Chiribiquete. "Flowers greenish yellow. Plant 5 ft. tall, becoming bushy." May 15–16, 1943, *Richard Evans Schultes 5441*.

Apocynaceae

Ambelania Markgrafiana *Monachino* in Lloydia 8 (1945) 122.

The three known collections of *Ambelania Markgrafiana* from Colombia indicate that the species is rather widely distributed, though rare, in the Colombian Amazonia. It is also known from the western Amazonas of Brazil.

Ambelania Markgrafiana is of no commercial importance. Its latex does not have the qualities which might make it of value as a chicle. It is, however, often used to adulterate the latex of *Couma macrocarpa* Barb. Rodr. which is employed in the manufacture of chewing gum. According to elderly members of the Witoto tribe who recall the days of the infamous Putumayo atrocities of the Casa Arana, the latex of both *Ambelania Markgrafiana* and *Couma macrocarpa* was added to that of *Hevea* in an attempt to satisfy over-exigent rubber exploiters.

At the present time, the Witotos of the Karaparaná and Igaraparaná Rivers paint their legs and arms with a coating of *Ambelania* latex as a protection from the millions of gnats or "jejenes" which, at certain seasons, abound in many localities of the Amazonas.

Colombia: Comisaría del Vaupés, Río Vaupés, Pucarón, alt. 240 m. "Arbol de 10 m. que crece grueso, con mucho látex blanco: corola amarilla, lóbulos parduzcos; frutos grandes, comestibles, aromáticos." October 2, 1939, *J. Cuatrecasas 7129*.—Intendencia del Amazonas, path between El Encanto and La Chorrera. "Tall tree, 20 m. Basal diameter 1 ft. Bark black. Very abundant latex, white. Fruit edible, sweet, yellow-green. Witoto name: *do-ko-gay*." May 31–June 2, 1942, *Richard Evans Schultes 3877*.—Comisaría del Vaupés, Upper Apaporis basin, between ríos Itilla and Macaya, near Corinto. "Slender tree 50 ft. tall. Very abundant, thick, white latex. Bark thin,

smooth with black and grey patches. Basal diameter 1–1½ ft. Nom. vulg. *palo de leche.*" April 1–7, 1943, *Richard Evans Schultes 5357.*

Rubiaceae

Cephaelis barcellana (*Muell.-Arg.*) *Standley* in Field Mus. Publ. Bot. 8 (1930) 184.

Known from Amazonian Brazil and from the Territorio del Amazonas of Venezuela, *Cephaelis barcellana*, although enumerated by Standley in "The Rubiaceae of Colombia," apparently had not hitherto been collected in the Republic. The collection, *H. Antonio Camilo 85*, from Florencia, Comisaría del Caquetá, is also probably referable to *Cephaelis barcellana* and would widen the known range of this species in Colombia.

Colombia: Comisaría del Putumayo, Río Putumayo, trocha entre Puerto Ospina y Concepción, alt. 250 m. "Flowers white. Bracts red and yellow." April 20–23, 1943, *Richard Evans Schultes 3678.*

Duroia hirsuta (*Poepp. & Endl.*) *K. Schumann* in Pringsh. Jahrb. Wiss. Bot. 19 (1888) 361.

The type of *Duroia hirsuta* was collected in Villavicencio. Although known from Amazonian Brazil, this species has apparently never been recorded from the Amazon drainage-area of Colombia.

This small tree occurs in dense forests, but I have never seen it growing individually. It forms colonies of twenty or more and invariably nothing grows underneath except *Selaginella.* Known widely in Amazonian Colombia as *solimán*, *Duroia hirsuta* is believed by the Indians to be a plant whose roots "poison" all other plants. Thus they explain the curious ecological phenomenon of the absence of other plants in colonies of *Duroia hirsuta.* The real reason may have some connection with the fact that the swollen internodes of the treelet are inhabited in all cases by ants.

Colombia: Comisaría del Vaupés, Apaporis River, near confluence

of Ajaju and Macaya. "*Solimán.*" January 1944, *Gabriel Gutiérrez & Richard Evans Schultes 612.*

COMPOSITAE

Gongylolepis maroana *Badillo* in Bot. Soc. Venez. Cienc. Nat. 8 (1943) 237.

The collections cited below are extremely significant because they place the genus *Gongylolepis* for the first time far within Colombian territory and very greatly extend to the southwest the known range of this species.

Gongylolepis maroana was described from material collected by Llewelyn Williams at the town of Maroa on the Venezuelan side of the lower course of the Río Guainía. Therefore, coming from so near Colombian territory, this species was to be expected in Colombia, but Mount Chiribiquete is fully 500 kilometers to the southwest. *Allen 3167* and *Schultes 5740A* are very good matches for the type, the only other collection of this species.

Gongylolepis is a small genus associated with the ancient flora of the Guianan-Venezuelan land mass. The first species described was *Gongylolepis Benthamiana* Rob. Schomb. from the Mazurini River drainage-area in British Guiana. Recently, Blake described *Gongylolepis glaberrima* and *G. crioclada* from Mt. Duida. The fourth species, *Gongylolepis maroana*, is the westernmost representative of the genus. The two collections cited below emphasize the strong relationship between the mountains of the upper Apaporis and the Vaupés and the Duida-Roraima mass.

COLOMBIA: Comisaría del Vaupés, Río Vaupés, Yuruparí Falls. "Small tree—3 m., flowers deep, dull purple." November 10, 1943, *Paul H. Allen 3167.*—Comisaría del Vaupés, upper Apaporis basin. Macaya River, Mount Chiribiquete. Sandstone. Xerophytic conditions. Savanna. Alt. 400–1200 ft. above forest floor, 1350–2150 ft. above sea-level. "Low spreading shrub, with thick, coriaceous leaves. Very abundant." January 18, 1944, *Richard Evans Schultes 5740A.*

EXPLANATION OF THE ILLUSTRATIONS

PLATE XXXII. ROUPALA COLOMBIANA *R.E.Schultes.* A. Flowering branch, one half natural size. B. Buds, about two and one half times natural size. C. Flower, about three and one half times natural size. D. Fruit, one half natural size.

Drawn by ELMER W. SMITH

PLATE XXXIII. ROUPALA SAXICOLA *R. E. Schultes.* A. Flowering branch, one half natural size. B. Buds, about twice natural size. C. Flower, about four times natural size. D. Fruit, one half natural size.

Drawn by ELMER W. SMITH

PLATE XXXIV. CYNOMETRA ZAMORANA *R.E.Schultes* Fruiting branch, one half natural size.

Drawn by ELMER W. SMITH

PLATE XXXV. GRAFFENRIEDA FANTASTICA *R. E. Schultes & L.B.Smith.* A. Flowering branch, about one half natural size. B. Fruiting inflorescence, about one half natural size. C. Bud, about four and one half times natural size. D. Flower, about four and one half times natural size. E. Bark of older basal portion of trunk.

Drawn by ELMER W. SMITH

EXPLANATION OF THE ILLUSTRATIONS

PLATE XXXVI. (Upper figure). BEGONIA LUTEA *Smith & Schubert*. Habit photograph of the colony from which the collection *Schultes & López 10062* was made.

Photograph by R. E. SCHULTES

(Lower figure). GRAFFENRIEDA FANTASTICA *R. E. Schultes & L. B. Smith*. Photograph of the tree from which the type collection was made.

Photograph by R. E. SCHULTES

PLATE XXXVII. AMBELANIA MARKGRAFIANA *Monachino*. Flowering and fruiting branch of the plant from which *Cuatrecasas 7129* was collected.

Photograph by J. CUATRECASAS

ROUPALA
colombiana

R. E. Schultes

ROUPALA
saxicola

R. E. Schultes

E. W. Smith

CYNOMETRA

Zamorana

R. E. Schultes

PLATE XXXV

GRAFFENRIEDA
fantastica
R.E. Schultes & L.B. Smith

R.E. Schultes

Plate XXXVI

Plate XXXVII

NEW CONCEPTS IN STYRAX FROM EASTERN COLOMBIA

BY

JESÚS M. IDROBO[1] AND RICHARD EVANS SCHULTES[2]

THE identification of a number of plants from the isolated sandstone mountains of the upper Apaporis River basin in eastern Colombia has revealed a collection which represents a species of Styrax hitherto apparently undescribed. A distinct form of this species is represented by a collection from the ecologically similar sandstone mesa at Yapobodá at the headwaters of the Cuduyarí, in the middle Vaupés River basin.

In the uppermost reaches of the Apaporis River, where the Ajaju and Macaya join, there are a number of grotesquely eroded quartzite mountains which rise abruptly from the flat, extensive Amazonian forest surrounding them. They represent the westernmost remnants of an ancient, now disrupted, mountain-mass which has its center in southern Venezuela and the Guianas. They can be followed westward and southwestward throughout the Colombian Amazonia where, across the Comisarías del Vaupés and Caquetá, there are extensive flat-topped ridges, isolated from each other often by many hundreds of kilometers. These ridges extend west as far as the upper Apaporis basin and San José del Guaviare, and southwest to the Falls of Araracuara on the Caquetá River (famous as Martius' westernmost collecting station and the type locality of many endemics) and La Chor-

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rera on the Igaraparaná River. Yapobodá, part of this broken range, is of special interest because, in the vast and sparsely explored Comisaría del Vaupés, it is located about midway between the westernmost mountains in the Apaporis and the Duida mass in Venezuela.

In many other localities in Amazonian Colombia, one finds distant and very indistinct outliers of this ancient formation in the form of small areas of white sand with a low caatinga-forest or savanna vegetation. So indistinct topographically are some of these formations that it might be difficult geologically to identify them with the ancient Venezuela-Guiana land-mass were it not for the fact that their flora is so strikingly different from that of the surrounding Amazon jungle and so similar to that of a number of analogous areas in southern Venezuela and in the Guianas. It can be shown that these isolated patches have an ancient remnant flora which is most closely allied to the flora of the Duida-Roraima ranges and of other peaks in the same far-distant mountains on the northern rim of the Amazon Valley.

As an example of these indistinct outliers, we may cite the rather extensive caatinga-forest between the headwaters of the Hamacayacu and Cotuhé Rivers in the interior of the *trapécio amazónico* (near Leticia). Similar areas occur near Mishuyacu and at Iquitos in Peru and at São Paulo de Olivença on the upper Amazon River in Brazil.

It is, therefore, apparent that a thorough study of the floras of these isolated mountains in eastern Colombia is of the utmost importance for a complete understanding of the origin and composition of the flora, not only of the Amazonas of Colombia, but also of large sectors of southern Venezuela, the Guianas and northern Amazonian Brazil. There would seem, likewise, to be some connection between this ancient flora rimming the north of the

Amazon Valley and that of the geologically old plateau which gives rise to most of the great southern tributaries of the Amazon. This might explain the apparently anomalous occurrence in northwesternmost Amazonia of rare elements which have their greatest diversification in southeastern Brazil; or, as in the case of the concept herein described, the close relationship of some species known from these two widely separated areas of central South America.

Mount Chiribiquete, the type locality of the *Styrax* which is herein described, has yielded a number of striking endemic plants and numerous species which exhibit a definite relationship with elements known only from Mounts Duida or Roraima. *Styrax rigidifolius* is one of the few species from the shrubby cover of the flat summit of Chiribiquete which does not seem to have a close ally in the northern Amazon region or on the Venezuela-Guiana land-mass. It is not common but grows hidden with the more abundant *Graffenrieda fantastica* Schultes, & Smith, *Ficus chiribiquetensis* Dugand, *Hevea nitida* Muell.-Arg. var. *toxicodendroides* (Schultes & Vinton) Schultes, *Roupala saxicola* Schultes, *Senefeldera chiribiquetensis* Schultes & Croizat, *Bombax coriaceum* Mart. & Zucc., *Vellozia phantasmagoria* Schultes, several Vochysias, numerous species of *Clusia*, an interesting *Ternstroemia*, and an undescribed species of *Leitgebia*. All of these plants are completely adapted to xerophytic conditions and high radiation, and, in this connection, it is interesting to note that *Styrax rigidifolius* itself has unusually rigid-coriaceous leaves with a very strongly inrolled margin.

There has been no species of *Styrax* recorded from Mount Duida. The only member of the genus reported from Mount Roraima is *Styrax roraimae* Perk., an endemic of this peak; it bears no relationship to *Styrax*

rigidifolius. *Styrax rigidifolius* would not seem to be closely allied to any known species, but it approaches most closely *S. ambiguus* Seub. of southeastern Brazil. If we are to judge from the description and a photograph of the type, *Styrax ambiguus* is very similar vegetatively to *S. rigidifolius* in having rather coriaceous or thick-papyraceous leaves of a small size with revolute margins, characters not common in the genus. There are, however, very appreciable differences in the size of the flower, the texture and indumentum of the calyx, the shape and size of the corolla lobes, the shape and size of the stamens, the pilosity at the point of union of the filaments with the corolla tube, and the form and pilosity of the ovary.

Styrax rigidifolius belongs to the section *Eustyrax*, series *Valvatae*. In the key to the species in Perkins' monograph (Pflanzenr. IV, 241 (1907)), the specimen which is here described as new traced out to the vicinity of *Styrax calvescens* Perk., an East Indian species with no relationship to *S. rigidifolius*.

Styrax rigidifolius *Idrobo & R. E. Schultes sp. nov.*

Frutex parvus, usque ad octo pedes altus. Rami teretes, cortice griseo, juniores fusco-pulverulenti, demum glabrescentes, usque ad 5–6 mm. in diametro. Folia petiolata, oblongo-elliptica, longe acuminata, apice ipso acuta, basi subrotundata vel saepe rotundato-cuneata, rigide coriacea, integra, fusco-pulverulenta, maturitate 6–7 cm. longa, 2.3–3 cm. lata, margine valde revoluta, supra glabra (ochraceo-viridia in siccitate) vel in nervo centrali basim versus paulo sordide pulverulenta, nitida, subtus cinnamomea, juniora rufidula, dense et molliter praecipue nervos versus tomentosa, pilis albis minutissimis stellatis remotius brunneis cum pilis aloëformibus intermixtis vestita, supra nervo centrali immerso, subtus valde elevato,

venis lateralibus sex ad novem, leviter arcuatis, minoribus subparallis et obscure reticulatis; petioli in vivo sulcati ut videtur, 6–10 mm. longi. Inflorescentiae racemosae, axillares, brevissimae, usque ad octofloraе, rhachide minute ferrugineo-tomentosa, bracteis caducis, minutis, linguiformibus, 2 mm. longis. Flores (specimine viso) 15 mm. longi, pedicello 5 mm. longo; calyx cupuliformis, coriaceus, margine truncatus, minutissime quinquedenticulatus, extus asper, valde minutissime stellato-tomentosus, 5 mm. altus, 4 mm. latus, margine obscure subundulato; corolla quinquepartita, tubo 3 mm. longo, quam lobi multo breviore, lobis in aestivatione valvatis ut videtur, vivo recurvis, membranaceis, apice utrinque densissime albo-stellato-tomentosis, apice paulo subcuspidatis, leviter marginatis, 13 mm. longis, 2.5 mm. latis; stamina decem, filamentis parte libera aliquid planis corollae tubo conniventibus et pilis fasciculatis albis grossiuscule atque dense obstita; antherae 7 mm. longae, 0.7 mm. latae, dorsaliter glabrae, ventraliter thecas versus albo-pilosae; ovarium superum, pyriforme, dense albo-tomentosum, 2 mm. in diametro; stylus stamina longitudine aequans. Fructus maturitate cinereo-viridis, quadrangulari-ovoideus, 8–10 mm. longus, 4–5 mm. in diametro, minute aspero-tomentellus, apice truncatus, breviter mucronatus, calyce persistenti; semen unum, interdum duo (?), rufo-brunneum, glabrum, oblongo-ovoideum, 7 mm. longum, 4 mm. in diametro.

Colombia: Comisaría del Vaupés, Macaya-Ajaju River confluence, Mount Chiribiquete. Quartzite base. Summit 800–1200 feet above forest floor; 1700–2100 feet above sea-level. "Low shrub. Flowers: petals white, recurved, anthers yellow. Fruit cupped, green." May 15–16, 1943, *Richard Evans Schultes 5468* (Type in U.S. Nat. Herb.; Duplicate type in Herb. Nac. Colomb.).

EXPLANATION OF THE ILLUSTRATION

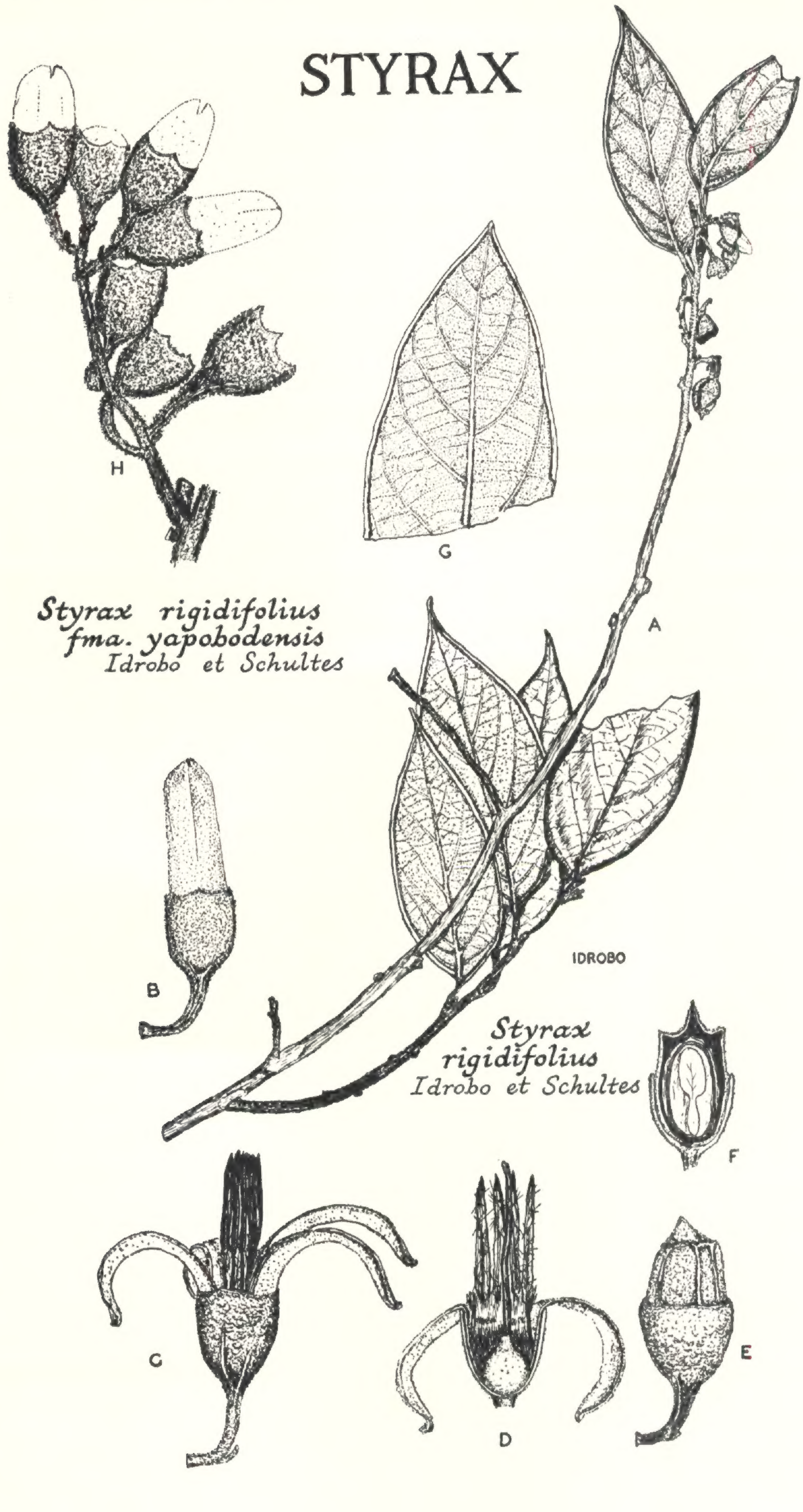
PLATE XXXVIII. STYRAX RIGIDIFOLIUS *Idrobo & R. E. Schultes*. A. Flowering branch, one half natural size. B. Bud, twice natural size. C. Open flower, twice natural size. D. Dissection of flower, twice natural size. E. Young fruit, twice natural size. F. Young fruit showing embryo, twice natural size.

S. RIGIDIFOLIUS forma YAPOBODENSIS *Idrobo & R. E. Schultes*. G. Portion of leaf, one half natural size. H. Inflorescence with bud, twice natural size.

Drawn by JESUS M. IDROBO

PLATE XXXVIII

STYRAX



Styrax rigidifolius fma. yapobodensis
Idrobo et Schultes

Styrax rigidifolius
Idrobo et Schultes

Styrax rigidifolius forma **yapobodensis** *Idrobo & R. E. Schultes forma nova.*

A *Styrace rigidifolio* foliis majoribus, marginibus revolutioribus, cum apice acuto non longe acuminato, supra opacioribus, subtus rufioribus; alabastris minoribus; calycibus grossiuscule quinque-sinuato-denticulatis; atque foliorum et calycum indumento asperiorio et rufiore differt.

This *forma* appears to be an ecological adaptation to the extreme xerophytism of the sandstone mesa at Yapobodá. An examination of the interesting plants collected at Yapobodá by Allen and a comparison of them with those of Mount Chiribiquete indicates that an even more severe xerophytism exists at the former than at the latter locality. As an example, the collection *Allen 3190*, referable to *Bombax coriaceum* Mart. & Zucc. but with extraordinarily reduced leaves, may be cited.

The differences enumerated above in the description of the form would, for the most part, seem to be related to adaptation to extreme xerophytism and radiation.

COLOMBIA: Comisaría del Vaupés, [Cuduyarí River], Yapobodá. "Tree 5 m. Flowers white." December 10, 1943, *Paul H. Allen 3232* (TYPE in U.S. Nat. Herb. 1951983).